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PHORONIS ARCHITECTA:

ITS LIFE HISTORY, ANATOMY, AND BREEDING HABITS.

BY

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INTRODUCTORY NOTE BY W. K. BROOKS.

As my name appears on the title-page of this Memoir as joint author, I take this opportunity to say that my own share in the work has been that of instructor and director only. The investigations are the exclusive work of Dr. R. P. Cowles, and while I have followed them in detail, and hold myself responsible for their soundness and accuracy, the credit for the research belongs to Doctor Cowles alone.

DRY TORTUGAS, FLORIDA, *July 3, 1905.*

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PHORONIS ARCHITECTA: ITS LIFE HISTORY, ANATOMY, AND BREEDING HABITS.

INTRODUCTION.

The study of *Phoronis architecta* was begun in the summer of 1901 and continued in the summer of 1902 at Beaufort, N. C. We are indebted to the Hon. G. M. Bowers, United States Commissioner of Fisheries, for the privilege of working in the Commission's station at Beaufort, where all the conveniences necessary for scientific investigation are at hand; to Prof. H. V. Wilson, director of the station in 1901, and to Dr. Caswell Grave, director during 1902, for many kindnesses.

While the study of the live material was for the most part done at Beaufort, the rest of the work was pursued in the zoological laboratory of the Johns Hopkins University.

Since the discovery of *Phoronis hippocrepia* by Wright in 1856, the affinities of this interesting genus have been more or less under discussion. Different investigators have sought to ally the Phoronidæ with the *Bryozoa*, the *Brachiopoda*, the *Sipunculida*, and other groups.

Roule (20) thinks that the Phoronidæ should be placed next to the Bryozoa in a natural classification. He does not consider that they have any affinity to the *Enteropneusta*, but from a study of the early stages of development he finds that they are related to the true *Chordata* (tunicates and vertebrates). He says, "lémbryon de Vertébré est une Trochophore renversée."

Lankester and McIntosh are inclined to consider *Phoronis*, *Cephalodiscus*, and *Rhabdopleura* as related forms, while Harmer (7) makes a comparison of *Phoronis* with *Cephalodiscus* and thinks that perhaps there may be some affinity.

Masterman (15, 16) in a series of papers made a comparison of the actinotrocha larva of *Phoronis* with *Balanoglossus* and its larva and also with *Cephalodiscus*. In this paper, he arrives at the conclusion that there is a close genetic relationship between the Phoronidæ, *Balanoglossus*, and *Cephalodiscus*. Since the appearance of Masterman's papers, Ikeda (9) has investigated the development of *Phoronis ijimai* and has made a careful study of several *Actinotrochæ* found in Japanese waters. Shortly after this, Longchamps (12) published a comparative study of the early development of several species of *Phoronis* and also of several species of *Actinotrocha*, giving a very careful critical résumé of the work done by different investigators.

Menon (17) has lately published a short paper on the *Actinotrocha*, in which he considers the Phoronidæ to be related to the *Chordata*, but thinks the relationship is to be traced through a form like *Rhabdopleura*.

This study of the development and anatomy of *Phoronis architecta* was begun before the publication of the last four papers mentioned, and when they appeared the abandonment of this investigation was seriously considered. However, since there seem to be specific differences and since there are several disputed points in the development, it seems best to publish the results of this study.

It is hardly necessary to enter into an historical account of the work that has been done on the development and anatomy of the Phoronidæ, since there are several papers which have reviewed the subject exhaustively.

METHODS.

Most of the material—eggs, larvæ, and adults—was fixed in a saturated solution of corrosive sublimate, to which had been added 2 per cent of glacial acetic acid. A fresh solution was made as soon as the fine white precipitate appeared, which is usually present in old solutions. This fixing agent gave very good results. Material fixed in Perenyi's fluid was found more valuable in some few respects than the acetic sublimate. When segmentation stages were treated with a 5 per cent solution of formaldehyde, the blastomeres stood out almost as distinctly as in the living material. The larger species of the two *Actinotrocha* found in Beaufort Harbor is much more active than the other, and when it comes in contact with the fixing fluid the preoral lobe is bent upward into an unusual position. Consequently a few drops of 4 per cent solution of muriate of cocaine in 50 per cent alcohol was added to the water containing the *Actinotrochæ*. After this treatment they died in their usual form when put in the fixing fluid.

Flemming's fluid, as well as the acetic sublimate, was found to be a very valuable fixing agent for the *Actinotrochæ*. Heidenhain's iron hæmatoxylin was used in staining sections of the adult, and a secondary stain of alcoholic eosin or rubin gave very good results. The most satisfactory stain for sections of young larvæ and *Actinotrocha* was found to be a solution of safranin in anilin water. Since it was very desirable to make a study of the adults throughout the year, and as it was not possible to remain in Beaufort for this purpose during the winter and spring months, specimens were collected and sent to Johns Hopkins University at different times. Here they were placed in aquaria filled with sea water, which was kept in good condition by a rich growth of diatoms on top of a layer of sand. Not only did the diatoms keep the water from becoming polluted, but they also afforded abundant food for the *Phoronis*, so that healthy individuals with their lophophoral tentacles fully expanded were continually at hand for a live study. The authors are much indebted to Dr. Caswell Grave, the originator of the diatom method in rearing *Echinoderm* larvæ, for the use of his aquaria. Drew's modification of Patton's method for embedding and orienting eggs was used with fairly good success, although a large percentage of the embryos were broken during the process. Most of the embryos were cut into sections 3 μ thick, but for some purposes sections 2 μ thick were used.

BREEDING HABITS.

Andrews's (1) observations on *Phoronis architecta* bring him to the conclusion that either the sexes are separate in that species or that if the individuals are hermaphroditic the male and female elements mature at different times. Many specimens examined by us during May, June, July, August, September, and October, both by means of sections and when alive, showed in no case ovaries and testes occurring at the same time in an individual, but ovaries and testes undoubtedly occur together in the same individual in *P. australis*. Benham (2) has observed this, as we have also, in material sent to us by Mr. Ikeda.

During the month of January the peritoneal tissues surrounding the blood cæca is very abundant, but as a rule at this time no eggs or spermatozoa are found in it. In one individual out of some 20 or 30 a few ovarian eggs were found, however. All of these specimens collected in January were without lophophoral organs, and we kept many of them in aquaria until the 1st of May. At this time lophophoral organs began to make their appearance in some, while in others they were absent. In all the specimens, however, either ovaries or testes were present, as was also the case in specimens collected at Beaufort in the early part of May. Further reference will be made to the lophophoral organs and their relation to the breeding season under the section which deals with the structure of the adult.

The breeding season of *Phoronis architecta* extends from March or April to November or December. Ikeda (9) has stated that "the breeding season of *Phoronis ijimai* ranges through about half of the year, say from November to June or July." There seems to be a surprising difference in the time of breeding between these two species. The *Actinotrocha* at Beaufort are found throughout the summer and autumn, but they are especially abundant during August and September. Ikeda has suggested that *Phoronis* annually "changes its generation." It does not

seem probable that this is the case for *Phoronis architecta*, because full-sized adults are found throughout the year in Beaufort Harbor, and specimens were kept alive for fifteen months in the laboratory of Johns Hopkins University.

THE LAYING OF THE EGGS.

During low tide in the summer and autumn it was easy to collect from 100 to 150 specimens of *Phoronis architecta* during an hour or two. About one-half of these would usually have male reproductive organs and the rest female reproductive organs. The *Phoronis* were placed in glass crystallizing dishes and after about twenty-four hours many of the individuals began to lay—usually at night—but the eggs were not retained among the tentacles in a mass, as described by most investigators, but were swept gently away from the lophophoral crown by the ciliation on the tentacles and on the anal region, so that they settled near by on the bottom of the dish. Sometimes, however, the newly laid eggs were carried up and down the tentacles in currents caused by the cilia, and occasionally a few eggs were found grouped near the tips of the tentacles, being held there loosely by a small quantity of mucus-like material. At no time, however, were eggs and larvæ aggregated in definite masses, as described by Ikeda (9), nor were they brooded among the tentacles, as Masterman (16) has observed in the case of *Phoronis buskii*. That eggs and embryos were not found by Longchamps among the tentacles of "*Phoronis d'Helgoland*" is no doubt due to the fact that the same habit prevails in the above form that does in *Phoronis architecta*.

While the adults were laying, they were examined under the compound microscope. They showed large numbers of eggs which were floating freely back and forth in the body cavity as the animal contracted and expanded. Sections of adults in this condition show that all these free eggs contained the first polar body spindle. At intervals of about one minute an egg is extruded with considerable force from the nephridial opening, and in no case do the eggs at this moment have polar bodies. The wall of the nephridial ridge is transparent enough to see the eggs as they slip through the larger part of the nephridium. While passing through, they are pressed by the walls of the organ until they are about twice as long as broad (fig. 1). The fact that *Phoronis architecta* does not keep its eggs in masses within the tentacular crown, together with the fact that most of the individuals lay them at about the same time at night, makes it possible to preserve any one stage in the development of the embryo in sufficient quantity for a thorough study.

FERTILIZATION.

Ikeda (9) and Longchamps (12) made the observation that the eggs in the body cavity of the parent showed the spindles of the first polar body. This I found to be the case in *Phoronis architecta* (fig. 1). Eggs in the nephridia were found to be in the same stage, and in neither case was there any sign of an entering spermatozoon or a male pronucleus (fig. 1). There is no doubt of the fact that in *Phoronis architecta* the spermatozoon does not enter the egg until the latter has been expelled from the nephridium. Ikeda observed this fact for *Phoronis ijimai*.

SEGMENTATION.

The eggs of *Phoronis architecta* while still in the body cavity are somewhat irregular in shape, and, as mentioned above, are decidedly so while passing through the nephridium. However, after they are laid they become almost perfectly spherical and average 100 μ in diameter (fig. 2), thus measuring the same as the egg of "*Phoronis de Naples*." (Longchamps (12).) The egg is very opaque, being heavily laden with small yolk granules. It is surrounded by a delicate membrane, which, however, is not very conspicuous, being closely applied to the surface, but after fertilization it separates to some extent (fig. 2).

Observations on the segmentation of the egg of *Phoronis* are conflicting. This part of the development of *Phoronis* seems to have been treated hastily by most observers, probably because it is difficult to obtain sufficient material for its study. It is agreed that the segmentation is total. Foettinger (5) and E. Schultz (21) claim that the segmentation is unequal.

Caldwell (3) says that in the four-cell stage two smaller clear and two larger opaque cells are present. Masterman (16) finds that in the four-cell stage the blastomeres taper toward one pole, and that this results, when the third furrow appears, in the upper four being less in bulk than the lower four. Masterman's description, I find, applies to the eggs of *Phoronis australis.* Ikeda (9) did not discover any appreciable difference in the size of the blastomeres until the eight-cell stage. At this time, he says, "it will be seen that the upper four blastomeres are very slightly smaller than the lower four."

In *Phoronis architecta* the first cleavage plane is meridional and usually divides the egg into two practically equal blastomeres (fig. 3), although sometimes the division is decidedly unequal (fig. 4). The cleavage furrow begins in the region of the polar bodies (fig. 5). After the completion of the first cleavage and sometimes before, the first polar body divides (fig. 6). In fig. 6 is seen the reconstruction of the nuclei after the first cleavage. Immediately before the second cleavage the two blastomeres, which were closely applied to one another after the first cleavage, come to overlap. About fifteen minutes after the first cleavage the second cleavage takes place. It is meridional and at right angles to the first, dividing the two equal blastomeres into four equal blastomeres. As Ikeda has observed, the cleavage does not occur simultaneously in both blastomeres nor does it in later cleavages (fig. 7). The blastomeres of the four-cell stage which at first overlapped soon become applied to one another so that the two meet in a cross furrow (fig. 8). Shortly before the third cleavage occurs the cross furrow disappears and the blastomeres come to overlap. The third cleavage takes place fifteen minutes after the second cleavage, and it is equatorial. The blastomeres become drawn out into a more or less ovoid shape and, as division takes place, the upper four blastomeres become rotated in the direction of the hands of a watch (fig. 9). The eight blastomeres are approximately the same size, as a rule, and there is a small segmentation cavity present which from now on persists (fig. 10). The three polar bodies are distinguishable at this stage sometimes within the blastocœle and sometimes on the surface of the blastomeres. The blastocœle is open at the animal and vegetal poles. The sixteen-cell stage arises from the eight-cell stage by a meridional division of each of its blastomeres, but they do not all divide simultaneously (fig. 11), although the difference in time is very slight. After the sixteen-cell stage the individual blastomeres were not followed. The division takes place rather irregularly, but the blastomeres are all about of the same size.

The so-called "blastocœle pore," observed by Ikeda (9), was found occasionally in young blastulæ, but it does not seem to be of constant occurrence nor definite in position (figs. 12, 13).

Two hours after the first cleavage the blastula is composed of seventy or eighty cells, and it is still inclosed in the egg membrane. Four hours later the membrane disappears, and the ciliated blastula begins to swim (fig. 14).

The blastomeres were so much alike and so uniform in size that their individual history was not traced. It would seem probable from Masterman's work on *Phoronis buskii* (16) that the cell lineage might be followed in that form, for he finds considerable difference in the size of the blastomeres in the early stages of cleavage at least.

The apical pole of the ciliated blastula is provided with long cilia (fig. 14). The nuclei are situated nearer the outer than the inner surface, and the inner ends of the cells are filled with rather dense granules. In the segmentation cavity are found the so-called "corpuscles," which have been observed by most investigators working on the early stages of *Phoronis.* Caldwell's (3*a*) view that they are not mesoderm cells is undoubtedly correct. Our observations agree with those of Ikeda (9), for the "plasmic corpuscles" are much smaller than any of the cells of the blastula, and none with nuclei were found. In *Phoronis architecta* they do not appear until the late blastula stage (fig. 14), at which time the inner ends of the cells are densely granular. It seems very probable that the corpuscles are pushed out from the densely granular part of the cell, and that, as Caldwell and Ikeda have held, they are an extra supply of nourishment.

The blastulæ, gastrulæ, and young larvæ of *Phoronis architecta* are quite similar in appearance to those of *Phoronis d'Helgoland* which Longchamps (12) has figured. The development is more regular than that of most other species, which is probably due to the fact that the eggs and embryos are not harbored in the tentacular crown.

GASTRULATION AND FURTHER CHANGES IN THE FORM OF THE LARVA.

In the blastula, which has just begun to invaginate, the invagination is eccentric, thus giving the first indication of the bilateral symmetry of the larva. This is further emphasized in the young gastrula of *Phoronis architecta* by a thickening of the ectoderm cells, which becomes the ganglion of the *Actinotrocha*. The cells composing this thickening of the ectoderm are at the apical pole in the blastula and they bear long cilia, but as gastrulation takes place and as the embryo elongates the thickening comes to occupy a position nearer the anterior end of the larva (figs. 15, 15*a*, 15*b*). The published accounts seem to indicate that the ganglion makes its appearance much later in most species than it does in *Phoronis architecta*, although Roule (20) figures the "plaque cephalique" at a rather early stage in *Phoronis sabatieri*. The changes which take place in the shape of the blastopore are much like those described by other investigators. At the beginning of gastrulation the blastopore is wide open and circular in outline. The lateral lips of the blastopore then gradually draw together in the posterior region, inclosing that part of the wall of the archenteron between them (fig. 20*e*), which becomes a solid mass of cells continuous with the cells of the fused lips of the blastopore (figs. 18*d*, 18*e*). The cells of the solid mass are of the same character as those of the wall of the archenteron where the blastopore is open. They are quite granular, except at the periphery, where they project into the cavity of the blastocœle, and their nuclei are quite indistinct. Both of these facts are characteristic of the cells, making up the archenteric wall (fig. 18*e*).

As a result of the closing up of the blastopore posteriorly, the blastopore becomes oval in shape, and an indication of a ventral furrow, first observed by Caldwell and called a "primitive groove," appears. In *Phoronis architecta* this groove is only to be seen in one or two sections back of the blastopore, after which the ventral surface is convex (figs. 18*d*–20*e*). A "primitive streak," as described by Caldwell (3*a*) could not be made out. The gastrula, which is at first circular in horizontal section, becomes slightly elongated when the blastopore takes on anzoval shape.

Gradually the blastopore lips close up more anteriorly until the blastopore becomes circular in outline but much smaller than it was originally. At the same time the anterior end of the larva begins to bend in a ventral direction and the archenteron becomes elongated posteriorly (fig. 20).

Now the larva increases slightly in length (fig. 21), the blastopore assumes the form of a transverse slit, the anterior end bends farther ventrally, and the posterior end of the enteron becomes applied to the ectoderm at the posterior end of the larva (fig. 21).

Our observations on *Phoronis architecta* agree with the description of Masterman (16), Ikeda (9), and Longchamps (12) in regard to the closure of the lips of the blastopore and the resulting change in the shape of the latter, but in *Phoronis architecta* the definitive blastopore does not seem to be pushed farther anteriorly by the special activity in the posterior region of the blastopore, as Ikeda has found to be the case for *Phoronis ijimai*. The definitive blastopore seems to be represented by the anterior part of the wide circular blastopore of the young gastrula. Its change in position with reference to the anterior end is due to an elongation of the posterior portion of the embryo and the ventral flexure of its anterior end.

Our studies on the development of *Phoronis architecta* lead us to agree with Ikeda and Longchamps as to the fate of the cells in the posterior part of the blastopore and as to the ectodermal origin of the "posterior pit." The cells of the posterior part of the blastopore become invaginated by the closure of the blastopore lips and form part of the ventral wall of the enteron, while the "posterior pit," which appears in *Phoronis architecta* shortly before the definitive blastopore is formed, is of ectodermal origin and has no apparent relation to the ventral groove. As Ikeda (9) has stated, the pit is the beginning of the nephridium of the *Actinotrocha*. In a recent paper Masterman (16*a*) says that he has found the "posterior diverticulum" both in larvæ of *P. buskii* and *P. hippocrepia* and that he considers them to be the anlagen of the nephridia.

FORMATION OF THE MESODERM.

There is considerable difference of opinion among those who have investigated the embryology of *Phoronis* as to the origin of the mesoderm, and there seem to be no two whose descriptions agree, although Ikeda (9) and Longchamps (12), in their recent papers, arrive at the same conclusions, generally speaking.

The study of the eggs and larvæ of *Phoronis architecta* and those of *Phoronis australis* show that the great difference in the origin of the mesoderm, as Roule (20) and Masterman (16) see it, may be due, in a great part, to difference in the larvæ themselves.

The eggs and embryos of *Phoronis australis*, for which we are indebted to Mr. Ikeda, are very similar in appearance to those of *Phoronis buskii*, judging from Masterman's figures (16). Sections of the eggs and larvæ of the former show the development to be of the same general type as that of *Phoronis ijimai*, which Ikeda (9) has described.

The eggs and larvæ of *Phoronis architecta* are considerably different from those mentioned above. They are more regular in form, the blastocœle is much more spacious and the cells themselves are more regular in shape and arrangement. They are most similar in appearance to the early stages of *Phoronis sabatieri* studied and figured by Roule (20) and those of "*Phoronis d'Helgoland*" figured by Longchamps (12).

The formation of the mesoderm begins in *Phoronis architecta* as soon as the flattened side of the blastula begins to gastrulate. In a few cases round blastulæ are found, within the blastocœle of which are rather large granular spherical bodies much larger than the plasmic corpuscles described above. Each of these contains an opaque body which takes saffranin stain with readiness. A comparison of these bodies with the nuclei of the cells of the blastula wall convinces one at once that they are not nuclei. In fig. 14*a* a section through such a blastula is shown in which these bodies are seen within the wall of the blastula as well as inside the blastocœle. They are embedded in the wall without reference to the limits of the cell and usually occupy the width of two cells. The cells inclosing these peculiar bodies do not differ from the cells surrounding them in that region and each has its own nucleus. These bodies are not the cut ends of amœboid processes which Caldwell (3*a*) and Roule (20) observed, for such processes do not occur in the blastulæ of *Phoronis architecta*. We are unable to make any positive statement as to their fate, but it is very probable that they break up into the smaller plasmic corpuscles. Such bodies as the former might easily be mistaken for mesoderm cells, and we suspect that the "mesoderm cells" observed by Foettinger (5), Metschnikoff (18), and E. Schultz (21) in the round blastulæ were of the same character.

The work on *Phoronis architecta* indicates that the mesoderm which forms the lining of the preoral lobe and the collar cavities of the *Actinotrocha* arises from the lips of the blastopore. As to the origin of the lining of the trunk segment, we are still in some doubt, but we are inclined toward Longchamps's suggestion that some of the cells of the nephridial pit give rise to it. Caldwell (3*a*) also holds that the mesoderm arises from the endoderm, assuming that the "posterior pit" (nephridial diverticulum), which he considers to be one point of origin of the mesoderm, is of endodermal origin. Roule (20) derives most of the mesoderm from the endoderm, but also considers the "bandelettes mésoblastiques," which Schultz (21) first pointed out to be the same as the posterior diverticulum of Caldwell, as giving rise to mesoderm.

As is seen on referring to fig. 15, the flattened part of the wall of the blastula has become more than one cell thick. In fact active cell division has taken place. Yet most of these cells are destined to become the wall of the archenteron, and only a few are to give rise to mesoderm. Careful examination of many sections fails to show that mesoderm cells ever have their origin from the dorsal surface of the archenteron. In this respect the development of *Phoronis architecta* seems to agree with that of *Phoronis kowalevskii* as described by Caldwell (3*a*) and Longchamps (12), and that of *Phoronis buskii*, which Masterman (16) investigated. In *Phoronis architecta*, as in the form studied by Longchamps (12), the anterior and lateral borders of the blastopore are most active in giving rise to mesoderm (figs. 16 *a*, *b*, *c*, *d*, *e*, *f*). Most of it is

proliferated from the anterior end of the archenteron, and the power of producing the same seems to diminish gradually toward the posterior end of the blastopore lips in those gastrulæ where the round blastopore is just beginning to close up (figs. 16 *a, b, c, d, e, f*).

The mesoderm cells are very ameboid in character and are often seen in living specimens and sometimes in sections sending out long pseudopod-like prolongations, which become attached to the walls of the gastrula. By means of these ameboid movements they are able to crawl up the walls of the blastocœle.

We were unable to make out any structure in *Phoronis architecta* which could be interpreted as "archenteric diverticula," such as figured by Caldwell (3*a*) and Ikeda (9). Fig. 16*e* might be interpreted as showing these diverticula, but the condition there is hardly different from the arrangement of the mesoderm cells, which are being pushed out into the blastocœle in front of the blastopore (figs. 16, 16*b*). Caldwell first observed these structures in the gastrulæ of *Phoronis kowalevskii*, but Longchamps (12), who has recently carefully studied the same species, has been unable to find them. Ikeda (9), however, finds very definite diverticula in the gastrulæ of *Phoronis ijimai*, but he figures them as being in the region of the blastopore, while, according to Caldwell's (3*a*) figures, they are found posterior to the blastopore.

Let us return again to the mesoderm cells which lie anteriorly to the blastopore. These ameboid cells undoubtedly multiply while in the blastocœle, and in a gastrula where the blastopore lips have closed up somewhat so as to give an oval outline to the blastopore (fig. 18*f*) these cells have become arranged into a definite sac (figs. 19, 20*a*), which is later to form the lining of the preoral lobe. In no case were we able to find the least indication of an anterior unpaired diverticulum, which Masterman (16) says exists in the gastrula of *Phoronis buskii*. At this stage the cavity of the sac is small and is present only in front of the blastopore. The walls, however, are extended on each side into a lateral cord of mesoderm cells, which lies in the blastocœle at the side of the blastopore (fig. 18*f*). Some of the cells of the dorsal wall of the sac send out pseudopodia, which attach themselves to an ectodermal thickening, and this thickening will become the ganglion of the *Actinotrocha* (fig. 19).

The above condition continues until the oval blastopore becomes smaller and round in outline (figs. 20, 20*c*), which change is also accompanied by further growth of the enteron in a posterior direction until it almost touches the end of the larva. The cells of the two lateral cords of mesoderm have now increased in number, have arranged themselves so as to inclose a cavity, continuous with the cavity of the anterior one described above, and have become attached both to the lateral ectodermal wall and the lateral endodermal wall (fig. 20*b*). Anteriorly this sac, which is now horseshoe shape (fig. 20*c*), is still only attached to the ganglionic thickening and the ventral ectodermal wall (fig. 20). The conditions just described are not due to the shrinkage of the mesodermal lining away from the wall of the larva, for the transparency of the living larva makes it possible to see the formation of the mesodermal sac. We have followed this formation step by step many times in the living gastrula and larva, as well as in sections and surface mounts.

As the anterior end of the larva bends farther ventrally and becomes a definite preoral lobe, the round blastopore assumes the shape of an oval with its major axis transverse to the long axis of the larva (fig. 21). The posterior part of the larva increases in length and the enteron sends out a posterior diverticulum, the beginning of the intestinal canal, whose blind end fuses with the ectoderm of the posterior end of the larva. The walls of the mesodermal sac become applied to the walls of the preoral lobe more generally, thus forming a definite mesodermal epithelium for the cavity of the preoral lobe (figs. 23, 21, 22). Posteriorly, as Masterman (15) has described for the fully developed *Actinotrocha*, the cavity is produced "into two horns running back laterally" (fig. 22*a*), but as yet there is no complete mesodermal lining in the cavity back of this (figs. 22 *b, c*). The posterior wall of the mesodermal lining of the preoral lobe forms a definite septum (figs. 21, 21*a*), but it is not as yet, at least, composed of two layers, as Masterman finds in the older *Actinotrocha*.

While the above changes have been taking place in the preoral end of the larva there has also been some change in the postoral region. It is seen from figs. 16 *c*, *d*, *e*, *f* that in the young gastrula with the large circular blastopore mesoderm cells are being pushed out into the blastocœle along both sides of the archenteric wall back almost to the posterior border of the blastopore. At this stage large spherical cells with rather small, deeply staining nuclei are sometimes seen floating freely in the blastocœle (fig. 17*a*). These cells have their origin in the wall of the archenteron (fig. 17) and are quite different from the bodies found in the blastocœle of the blastula. They have a definite nucleus and they seem to be similar cells to those found by Ikeda in the larva with one pair of tentacles. They certainly do resemble the blood corpuscles found in the older larvæ, only they are considerably larger. Ikeda (9) came to the conclusion that these cells were the "mother cells of blood corpuscles which are found as corpuscle masses in the collar cavity of the *Actinotrocha*." Since the publication of his paper Mr. Ikeda has written that he considers his theory concerning the fate of these cells to be incorrect. They are easily distinguishable from all other cells by the fact that they are larger and that the cytoplasm does not stain. They have a nucleus which is rather small. We shall return to a consideration of these cells when we describe the blood corpuscles of the *Actinotrocha*.

As the blastopore lips begin to close up posteriorly (figs. 18 *d*, *e*) the endoderm cells in that region lose the power of giving rise to mesoderm cells, but they are still found arising in a more anterior region.

At a little later stage, in which the blastopore has become circular again after the fusion of the blastopore lips and the enteron has almost reached the posterior end, a few mesoderm cells are seen lining the ventral ectoderm in the posterior region (fig. 20*d*). These cells, however, do not have their origin from the wall of the posterior part of the enteron nor from the ventral ectoderm which Caldwell (3*a*) would call the "primitive streak." The cells forming the ventral ectoderm are very regularly arranged into a layer one cell thick and all the nuclei are in a resting state. The mesoderm cells have either migrated from the cells of the lateral cords which are prolongations of the sac, forming the lining of the preoral lobe (fig. 20*e*), or from the region of the blastopore, where some mesoderm cells are still arising. In general, our interpretation of the facts bearing on the origin of the mesoderm in the posterior region of the larva agrees with that of Longchamps (12) for *Phoronis kowalevskii*.

When the larva reaches the stage shown in fig. 21 where the blastopore is transverse and the archenteron fuzes with the posterior ectoderm, the mesoderm cells are found to be more numerous in the posterior region, and in nearly all cases they are applied to the ventral suface of the blastocœle. At this time the proliferation of mesoderm cells from the endoderm has ceased in the anterior region and there is no indication of any mesoderm cells being given off from most of the posterior region. At the extreme posterior end of the enteron, however, a transverse section across the larva (fig. 22*d*) shows a mass of cells which might be taken for proliferating mesoderm cells. Traced farther back, this mass of cells is found to be part of the wall of the "posterior pit," or, as Ikeda (9) has called it, "the nephridial pit" (figs. 22 *e*, *f*, *g*). The fate of the cells of the nephridial pit will be discussed in the description of the larva with two tentacles.

Larvæ like the one just described do not show the least trace of a mesentery between the collar and trunk. In fact, one could hardly say that a trunk existed at this time. The oblique strongly ciliated tract of ectoderm which indicates the line of origin of the larval tentacles has not appeared.

FURTHER GROWTH OF THE YOUNG LARVA.

The flexure of the preoral lobe continues as the larva grows older (fig. 24). In this way a vestibule is formed and the original blastopore becomes the part which connects the vestibule and archenteron (fig. 24). This relation between the vestibule and blastopore has been recognized by Masterman (16), Roule (20), Ikeda (9), and Longchamps (12). Longchamps speaks of it as a "stomodæum," and Masterman does also, but the latter adds "œsophagus" after it. (If our

idea that a stomodeum is a pitting in of the ectoderm which finally breaks through into the enteric cavity is correct, then Masterman's and Longchamps's use of the word is incorrect.)

Masterman speaks of a "slight ridge" running around the edge of the preoral hood and then "downwards till it is lost on the surface of the tentacles." Such a ridge is not present in the larva of *Phoronis architecta* and there is no connection between the ciliated tract along the line of which the larval tentacles arise and the ciliated edge of the preoral hood.

At this stage (fig. 24) a definite intestinal canal is seen which, however, does not open yet to the exterior. The intestine, as described above, is not of ectodermal origin in the larva of *Phoronis architecta*. There is no proctodeum. On this point our observations agree with those of Masterman, Longchamps, and Ikeda.

Roule (20) says: "Un anus et rectum se façonnent, aux dépens de l'ectoderm, sur l'extrémité postérieure du corps" (p. 102), and Caldwell (3*a*) derives the intestine from the remains of the "primitive streak."

As yet the anal papilla is not at all definite, but the ciliated band along which the larval tentacles are to arise has now appeared. This is indicated in the sagittal section (fig. 24) by a thickening of the ectoderm.

The mesoderm cells which in fig. 21 are seen applied to the ventral ectoderm of the larva have now increased considerably in number and have become arranged at quite definite intervals (fig. 24). If the ventral surface of the larva is examined, while the larva is alive, it will be seen that these cells have become simple muscle cells made up of two rather delicate fibres which extend from a large nucleus situated near the mid-ventral line. These fibres run parallel to one another around the wall of the larva (fig. 25).

The whole body cavity back of the mesentery between the cavities of the collar and lobe represents the larval collar cavity of the *Actinotrocha*, and although its somatic walls are not lined by a perfectly continuous mesodermal epithelium, yet there are indications that such a lining is being formed. The ventral and lateral walls of the stomach, however, are perfectly free from any epithelial covering. In fact, in all the Actinotrochae examined no mesodermal epithelium covering the ventral and lateral walls of the stomach in the collar region could be found. We have never seen any sign of mesodermal sac-like formation such as occurs in the preoral lobe.

Roule (20, p. 112) has described in a considerably older larva than the one with which we are dealing certain mesodermal cells to which he has given the name "conjunctivo-musculaires elements." These he represents as spindle-shaped cells terminated by long fibre-like prolongations and he has figured them as being quite numerous in the "plasma, transparent et consistant," of the coelomic cavity. While the young larva of *Phoronis architecta* bears a close resemblance to that of *Phoronis sabatieri* described by Roule (20), yet at no time during the life of the larva have we seen these cells suspended in the body cavity in such numbers as he has shown. Spindle-shaped cells with long prolongations are quite numerous, but they are usually found applied to the somatic walls of the larva.

Although recent investigators have thrown some doubt on the existence of the lobe-collar septum, yet such a septum unquestionably exists in the larva of *Phoronis architecta*. Ikeda (9) has shown that it is incomplete in the old actinotrocha and our observations agree with his, but it is a fact, nevertheless, that the septum is continually present throughout the larval life of *Phoronis architecta* and that it makes its appearance at a very early stage in the life history.

Longchamps (12) says: "Si une subdivisions plus ou moins complète s'établissait, entre ces deux regiones, elle ne seriat en tout cas que secondaire, et la cloison s'édifierait aux dépends de mésenchyme." It is plain from what has been said that we can not agree with Longchamps in his statement that the septum is secondary. It must be admitted, however, that the septum between the lobe and the collar is often considerably thinner than that between the collar and the trunk. If its origin had not been followed from the earliest stages by means of sections in three different planes, whole mounts and live material, we should not have been inclined to consider it a primary and constant organ of the larva.

We had confidently expected to find in the larva of the stage represented in fig. 24 some indication of the mesentery between the collar and the trunk, but were disappointed. Although the ciliated tract along which the tentacles are to arise has made its appearance and extends obliquely around the body proper of the larva, indicating a line just a little above the line of separation of the cavities of the trunk and collar in the older actinotrocha, yet examination of sections does not show the least sign of the mesentery or its fundament.

Ikeda (9) has found mesoderm cells connecting the nephridial canals with the splanchnic walls, and he thinks they are the first indication of the septum between the collar and trunk cavities. We have not been able to find the paired masses of "hypoblast cells" which Masterman (16) says give rise to the trunk cavities, although it is true that mesoderm cells were found lying on the dorsal wall of the intestine. Masterman does not follow the fate of these masses, but in the larva with three pairs of tentacles he speaks of "the two mesocœles pushing dorsally, their walls forming a pair of conspicuous mesenteries with the walls of the metacœles" (p. 395).

As has been said, the masses of cells that Masterman (16) speaks of have not been found, but we do not deny that the condition which he describes may exist in the larva of *Phoronis buskii* with three pairs of tentacles.

"*Nephridial pit*" (Ikeda).—A structure of the larva of *Phoronis* which has given rise to considerable controversy is the "nephridial pit" ("posterior, anal, ectoblastic pit," "posterior diverticulum"). It seems safe to assume that such a structure exists in the young larvæ of all species of *Phoronis*. It has been seen by Caldwell (3*a*) in *P. kowalevskii*, by Ikeda (9) in *P. ijimai*, by Longchamps (12) in *P. kowalevskii*, by Masterman (16*a*) in *P. buskii* and *P. hippocrepia*, and by us in *P. architecta*. Although Roule (20) has not observed the pit in *P. sabatieri*, it seems probable that such a structure will be found there on further investigation. It is difficult to believe that Roule's understanding of the origin of the nephridia from two cell masses of somatopleure symmetrically placed at the sides of the larva is correct. As stated above, we consider the pit to be of ectodermal origin (fig. 24). Further study of the structure leads us to agree with Ikeda that it divides into two lateral branches, each of which becomes a nephridial canal of the actinotrocha (figs. 25, 26, 27, 28). In fig. 25, which is a drawing made from a living larva, the canals, which in a little younger stage were practically the same diameter throughout their length, have become tipped at their distal ends with a bunch of cells which, we believe, are later to form the excretory cells of the nephridium.

No positive statement concerning the origin of these cells can be made, since it is difficult to obtain many larvæ of *P. architecta* which are old enough to show these bunches of cells in the process of formation. The sections examined afford no evidence that they are formed by free mesoderm cells attaching themselves to the internal ends of the nephridial canals, and we are rather inclined to consider them as arising from the cells of the internal blind ends of the nephridial canals (figs. 25–28). Ikeda's description (9) of the way the nephridial tubes arise from the ectodermal pit—i. e., by the "reevagination of the distal unpaired portion of the nephridial pit"—seems to be correct. Longchamps's (12) interpretation of the change in form of the "ectodermal pit" agrees quite closely with Ikeda's description.

"*Medullary plate*" (Roule).—When the young larva of *Phoronis architecta* has reached the two-tentacle stage cross sections show that there is a definite ventral ciliated band extending from the mouth to the ciliated tentacular band (figs. 29, *b, c, d, e*). This ventral ciliated band has been observed by Roule (20) in the larva of *P. sabatieri*, but it has not been described for any other species. Roule has homologized it with the medullary plate or medullary groove of the annelid larva.

"*Trunk cavity.*"—Longchamps has drawn attention to a figure of an *Actinotrocha* published in Hatschek's "Lehrbuch der Zoologie." In this figure are represented two cœlomic sacs surrounding the intestine. Hatschek does not describe the origin of these sacs, but Longchamps (p. 555) proposes the question, "Si les canaux ne dérivaient pas des expansions latérals du diverticule ectoblastique, chacun des canaux restant en rapport avec l'extérieur par un orifice

résultant du dedoublement de l'orifice primitif et médian, tandis que le restant du diverticule ectoblastique deviendrait la cavité postérieure du corps."

Such an origin for this posterior cavity would seem to be a possible one and would give an easy explanation for the origin of the collar trunk and ventral mesenteries.

We believe that the cavity of the trunk is formed in the following manner: As the tentacles grow out and increase in number the posterior region of the larva about the rectum increases greatly in length. In doing the latter the mesodermal lining of the collar is drawn away from the somatic wall in the region back of the tentacular band, and a cavity is left containing the rectum, part of the stomach, and the proximal part of the nephridial diverticula. At the same time this is taking place certain cells which seem to arise from the base of the nephridial diverticula give rise to the lining of the cavity of the trunk. As to the manner of origin of these cells we are still in doubt. We have not found two cœlomic sacs which Hatschek (8) seems to have figured (it is possible that his figure is meant to represent a single sac cut at two places), and we have hunted for them in larvæ where the diverticula are just beginning to form and also in larvæ with two, four, and six tentacles. In one specimen with two tentacles, however (fig. 30), an arrangement of mesodermal cells on the dorsal side of the intestine which seems to be the beginning of a sac is found; this, however, is not paired. Whether or not this sac and its cavity give rise to the lining and cavity of the trunk we can not say, for we have found but one specimen in which this condition exists.

One thing is certain, the fully developed trunk cavity of the *Actinotrocha* has a distinct mesodermal lining, consisting of a somatic and a splanchnic layer. As far as we know all *Actinotrochæ* have a ventral mesentery, which tends to support the view that the lining of the cavity of the trunk has its origin in a sac which grows around the rectum and posterior part of the stomach. Whether or not the fact that there is an indication of a dorsal mesentery in the posterior region of some of the fully developed *Actinotrochæ*, Species B., has any bearing on the double origin of the cavity of the trunk we can not say, for we have never seen the very young larvæ of this form.

The youngest larva taken from the tow had three pairs of tentacles, with beginnings of the fourth pair. In this larva the tentacles had grown considerably in length, and the posterior region had become somewhat elongated (fig. 31). Only one specimen of this age was obtained, and it was only studied while alive. The mesentery between the collar and lobe was plainly seen, and there seemed to be a thin mesentery between the region of the collar and the younger trunk region. The nephridial canals were seen with difficulty, but the rounded bunches of excretory cells forming the internal ends of the canals were plainly visible.

When the larva of *Phoronis architecta* has five pairs of tentacles (fig. 32) the trunk region is elongated considerably and constitutes about one-half the length of the larva. In fact, the larva at this stage looks much like the fully developed *Actinotrocha*. The "retractors" described by Ikeda (9) are now present and the body wall in the anal region shows a thickening which is to become the perianal ciliated band. This larva shows clearly the presence of two mesenteries.

In the larva with six pairs of tentacles (fig. 33) all of the organs of the fully developed *Actinotrocha* are present. The ventral pouch begins to invaginate (fig. 33) and sections usually show that the blood corpuscle masses are forming.

FULLY DEVELOPED ACTINOTROCHA.

There are two species of *Actinotrochæ* found in the waters of Beaufort Harbor, and they are very similar, if not identical, with the two species that E. B. Wilson (24) observed in Chesapeake Bay. From the latter part of May until the latter part of September both species are fairly abundant in the tow.

Wilson has designated the two species found in Chesapeake Bay as Species A. and Species B., and because of the general agreement between our observations and his descriptions the Beaufort *Actinotrocha* will be designated as Species A. and B., although we are satisfied that Species A. is the larva of *P. architecta*.

Species A.—Species A. (fig. 34) is somewhat smaller than Species B. and its average length is 1.03 mm. The trunk is quite stout, the intestine is short, and the posterior end of the stomach reaches as far as two-thirds of the length of the trunk cavity. When about ready to metamorphose, this larva usually has 18 larval tentacles and an equal number of young adult tentacles. The adult tentacles do not usually appear until the larva has 18 larval tentacles (its full number) and they arise as thickenings on the under side of the bases of the larval tentacles. In this respect the larva resembles one of the actinotrochæ which Ikeda (9) has described. The blood corpuscles are found in two masses usually applied to the ventro-lateral surface of the stomach, and they make their appearance in the larva with 12 or 14 tentacles. A pair of muscles which Ikeda has been the first to describe, and which he has called "retractor muscles," are always present: although they have not been made out in younger larvæ than those with 10 tentacles. This species is without the so-called "stomach diverticula." Pigment cells are found rather irregularly scattered on the wall of the body cavity. There are definite aggregations of these at the bases of the tentacles, and a few pigment cells are seen on the surface of the blood corpuscle masses. Usually there are quite a number in the wall of the posterior portion of the trunk.

This *Actinotrocha* is not as active as Species B. and it does not, as a rule, turn up its preoral hood when irritated. Its metamorphosis usually takes place quickly, fifteen or twenty minutes being required for its completion. *Actinotrocha* Species A. is, no doubt, the actinotrocha of *P. architecta.*

Species B. (*fig. 35*).—This *Actinotrocha* is larger than Species A., and when about ready to metamorphose it has an average length of 1.22 mm., and has at least 26 tentacles. (Wilson (24) figures the *Actinotrocha* Species B., ready to metamorphose, with 22 tentacles.) The difference in appearance between this larva and Species A. is rather striking. Beside being somewhat longer, it is slightly narrower in the collar region and decidedly so in the trunk region, which gives it a much more graceful appearance than that of Species A. The intestine is quite long, extending throughout the posterior two-thirds of the trunk cavity.

M. Longchamps has kindly pointed out to me that the "adult tentacles appear bilaterally, the mid-ventral line being, at first, free of the buds." They do not arise, however, as thickenings on the under side of the bases of the larval tentacles as in Species A. They have their origin at the base of the larval tentacles, but they are separate from them, and they appear first in the larva with 24 tentacles.

This *Actinotrocha* differs in three important respects from *Actinotrocha* Species A. In the first place it has its blood corpuscles aggregated into four masses, two of which are usually in the same position as the pair in the smaller species. The other two, however, are found, as a rule, more anteriorly in the collar cavity, and are applied to the dorso-lateral walls of the stomach. The posterior pair lying on the ventro-lateral sides of the stomach make their appearance during the 18 or 20 tentacle stage, but the other pair do not appear until about the 22-tentacle stage. This larva also has retractors extending from the ganglion to the region of the first and second pair of tentacles.

A second point of difference is the fact that *Actinotrocha* Species B. possesses a pair of diverticula at the anterior end of the stomach. These are present as early as the 22-tentacle stage. This larva can further be distinguished from the other species by the fact that there is found in the older larvæ a sensory papilla on the mid-dorsal surface of the preoral lobe.

Actinotrocha Species B. is much more active when irritated than the other species. The least irritation causes it to turn up its hood and to assume attitudes like those figured by Masterman (15). In fact, judging by the figures and text of Masterman's paper, it seems that there is considerable similarity between this larva and the one he has described. The two larvæ are very much alike in shape and both have the lateral stomach diverticula, but the form that Masterman describes has only two masses of blood corpuscles. The two species are not identical, nor is *Actinotrocha* Species B identical with *Actinotrocha branchiata* from the North Sea, for, as Longchamps has pointed out to us, the latter has but two blood corpuscle masses. Longchamps has informed us that in *Actinotrocha* Species B. the adult tentacles make their appearance in the

same special way that they do in *Actinotrocha branchiata* (found near Helgoland and described by J. Müller (19); and Masterman (15) says in his paper that the form he worked on "does not appear to differ in any essential respect" from *Actinotrocha branchiata*. There seems, however, to be considerable difference in size between *Actinotrocha branchiata* and *Actinotrocha* Species B., for, according to Longchamps, the best-developed specimen that he obtained of this species measured 2 mm., while the length of *Actinotrocha* Species B. averages 1.22 mm.

Although *Actinotrocha* Species A. seems to metamorphose without any difficulty when brought into the laboratory, yet we have never been able to induce *Actinotrocha* Species B. to do so. Specimens have been kept for ten days or more (the pouch and blood corpuscles being well developed) and in some cases they succeeded in evaginating the ventral pouch, but they were never able to complete the metamorphosis.

As far as we know, the adult of this *Actinotrocha* has never been found, but probably it lives under quite different conditions from *Phoronis architecta*, and it is not improbable that it may be found as a deep-water form.

INTERNAL ORGANIZATION OF THE FULLY DEVELOPED ACTINOTROCHA.

"*Subneural gland*" (Masterman).—Masterman (15) has described a depression in the dorsal wall of the buccal cavity which he terms a "subneural gland" and which he compares with the gland of the same name in the Tunicata and also possibly with the hypophysis of the Vertebrata.

Roule (20) and Ikeda (9) are of the opinion that this depression is a product of the fixing method.

Longchamps (12) does not consider it to be an accidental structure, but he does not agree with Masterman's view as to its theoretical significance.

Menon (17) says that the "subneural gland" first appears in connection with the collar and that during development it shifts forward into the preoral lobe, but in another part of his paper he says the œsophagus is often folded transversely (this also the case in the young *Phoronis*) into pouches and the "subneural gland" is a diverticulum of its dorsal wall.

While in examining sections we have frequently found a depression in the region that Masterman (15) indicates, we have never found it in the living larva. Only in very poorly killed larvæ have we found the depression to be as deep as Masterman has shown, and in all cases the structure of the wall is practically like that of the œsophagus.

In the *Actinotrochæ* Species A. and B. there is no depression in the living larva which might be homologized to the subneural gland of higher animals, and we are forced to agree with Roule and Ikeda in their belief that the so-called "subneural gland" which Masterman describes is a product of fixation.

"*Oral and atrial grooves*" (Masterman).—Masterman (15) has observed a mid-ventral ciliated area leading into the mouth from the preoral lobe in front and a broad ciliated area depressed into two oral grooves leading into it from the ventral surface of the collar area. He has also seen two so-called "atrial grooves" leading into the dorso-lateral corners of the mouth. Masterman says he does not find gill-slits in the *Actinotrocha*, nor does he find structures that he considers to be their homologues. "The atrial grooves" of the *Actinotrocha*, he says, however, are the analogues of gill-slits (15, p. 319). On page 358 (15), however, he says that "tentatively, I would regard the atrial grooves of the *Actinotrocha* as the early rudiments of pharyngeal clefts as found in Cephalodiscus."

His "oral grooves," he says, correspond to the oral grooves in *Cephalodiscus*.

Roule (20) does not find the "atrial grooves," but finds two lateral grooves, which he considers to be formed by the insertion of the hood on to the collar wall.

Ikeda (9) and Longchamps (12) are of the opinion that these grooves do not normally exist.

We have made a careful study of the live *Actinotrocha* and of surface mounts, but have not been able to make out these grooves in either Species A. or Species B. Sections, however, show that the "oral grooves" are present, and that in most preparations where the preoral hood has been turned upward by violent contraction (due to the fixing agent) there are two short grooves

in the position in which Masterman finds the "atrial grooves." In those cases in which the hood remains in its normal position we have seldom found Masterman's so-called "atrial grooves," and even in a few cases where the hood is turned upward they have been absent.

The ventral wall of the hood just as it passes into the wall of the œsophagus not infrequently shows a pair of bilaterally situated grooves which are similar to those found on the ventral collar wall.

"*Neuropore*" (Masterman).—See section on the nervous system.

"*Subneural sinus*" (Masterman).—Another organ which Masterman (15) has described is a sinus immediately below the nerve ganglion, caused by the want of contiguity between the mesoblastic walls of the preoral cavity and the collar cavity. This sinus, he claims, is closed except for a fissure which leads eventually into the dorsal blood vessel. He compares this sinus to the heart of Balanoglossus.

Menon (19), as far as we know, is the only other worker on the *Actinotrocha* who claims that there is a definite vesicle beneath the ganglion and he has discovered no connection between its cavity and the dorsal blood vessel.

Roule, Longchamps, and Ikeda do not find this organ, but the latter recognizes the existence of a space ("posterior recess") free from mesenchymatous fibres, which is the posterior part of the preoral lobe. This, however, he says, does not connect with the dorsal blood vessel.

From the study of the early development of *Phoronis architecta* and the origin of the mesentery between the hood and the collar, we have come to the conclusion that no vesicle is formed in that species between the two layers of the mesentery (if two layers exist). The mesentery which forms the posterior wall of the preoral lobe cavity is found attached just back of the ganglion in the median line and there is not the least sign of a vesicle other than the cavity of the preoral lobe (fig. 24).

In neither *Actinotrocha* Species A. nor *Actinotrocha* Species B. have we found a vesicle below the ganglion, although in both cases there is a space such as Ikeda (9) has seen, free from mesenchymatous fibres. The anterior boundary of this space is rather sharply defined and occasionally among longitudinal sections a fibre with a nucleus is seen running vertically from the dorsal to the ventral wall of the hood, giving the appearance of an anterior wall to the space. These fibres, however, are very much more delicate than the wall of the collar lobe septum, and what is more, they occur only occasionally and are evidently not sections through a membrane.

In the *Actinotrochæ*, which we have examined, there does not exist any vesicle beneath the nerve ganglion nor any structure which could be likened to the heart vesicle of *Balanoglossus*. For the supposed relation of the dorsal blood vessel to the "subneural sinus," see Blood system.

"*Stomach Diverticula*" (Ikeda, Longchamps, and Menon).

"*Notochords*" (Masterman and Roule).

Ever since Johannes Müller (19) saw the paired "blinddarme" in *Actinotrocha branchiata* nearly all of those who have studied *Actinotrochæ* have observed the same structures. Some have considered them to be liver diverticula, others have described them as dark masses with globules and as brown specks. Wilson calls them "glandular lobes of the stomach."

Ikeda (9), Longchamps (12), and Menon (17) speak of them as "stomach diverticula," but they do not ascribe any function to them. Masterman (15) and Roule (20) look upon them as rudimentary notochords. Roule, Ikeda, and Longchamps have studied larvæ in which the diverticulum was not paired and lateral, but unpaired and medio-ventral. The latter investigator has observed larvæ of both types.

We find that in Species A. the diverticulum is undeveloped even at the time of metamorphosis while in Species B. the diverticulum is paired, well developed, and ventro-lateral.

Longchamps has very justly objected to Masterman's use of the name "*Diplochorda*," under which the latter includes the Phoronidæ and *Cephalodiscus*.

The diverticula of Species B. do not show the regularly arranged vacuoles which Masterman has described for the *Actinotrocha* from St. Andrews Bay. In fact, we agree with Longchamps's (12) observations in finding the histological characters absolutely different in Species A. and B. from the histology of notochords, and there is not the least indication of supporting tissue.

However, larvæ which we have examined, fixed in Flemming's fluid, have not shown the vacuoles to be filled with fat droplets as Longchamps states.

Sections through the diverticula of quite old larvæ (fig. 35) stained with iron hæmatoxylin show columnar cells, nearly every one of which contains a deeply staining body about one-quarter the size of the nucleus. The bodies are not found in the wall of the stomach proper, and we believe that they give the yellowish-brown color to the diverticula of the live *Actinotrocha*.

In some cases we have found old larvæ in which the cells of the diverticula were vacuolated, but in these cases we have also found that the entire stomach wall was vacuolated. The vacuoles were never large enough or numerous enough to alter the natural position of the nuclei.

According to Masterman's description, the first vacuoles are formed at the distal ends of the cells and more vacuoles arise later between these and the inner ends of the cells. As far as we know, the origin of vacuolated tissue in vertebrates is the reverse of this, the vacuolization beginning at the center of the cord and traveling outward.

The specimens of *Actinotrocha* of *Phoronis sabatieri* which we have examined show the structure of the stomach diverticulum to be very similar to that of the diverticulum in the *Actinotrocha* Species B. The diverticulum, however, is somewhat more vacuolated in the former than in the latter, but it does not show the peculiar structure which Masterman has described for the "notochord" of the species from St. Andrews Bay.

It is hard to see what use the *Actinotrocha* has for any organ of support in the region where the diverticula are found and it seems much more probable that they have a glandular function.

Nervous system.—It is generally admitted among investigators who have studied the anatomy of the *Actinotrocha* carefully, that the creature has a subepidermal layer of nervous tissue throughout the body which is fibrillar in character. This nervous tissue assumes the form of quite definite tracts in certain parts of the body in *Actinotrocha* Species B. and fairly well-developed nerves can be said to exist. The most conspicuous ones are found in the median dorsal line of the preoral hood as three distinct longitudinal bundles of nerve fibres extending from the ganglion to the anterior edge of the hood. There are other tracts which, though they are not as definitely marked out as the above, are undoubtedly nerves.

Masterman (15) in his work on the anatomy of the *Actinotrocha* from St. Andrews Bay has described a complicated nervous system, but the investigations of Roule (20), Ikeda (9), and Longchamps (12) have thrown considerable doubt on the correctness of his observations. Whether these differences have been due to differences in the *Actinotrochæ* studied by these workers or whether they are due to the technique it is impossible to say, but, judging from the difference in the degree of development between the nervous system in Species A. and Species B., we are led to believe that the disagreements are due partly to the fact that no two of these investigators have studied the same species of *Actinotrocha*.

While the nervous system of Species A. can with careful study be shown to be very similar to that of Species B., yet it is so feebly developed that without first having studied *Actinotrocha* Species B. we should not have been able to see the similarity in the disposition of the different nervous tracts. The ganglion with its three dorsal longitudinal nerves running along the median line of the hood is easily seen in the live larva of Species A., but in sections we have found it impossible to trace the latter. The sensory papilla mentioned in the description of the *Actinotrocha* Species B. is absent in this species.

We are pleased to be able to confirm, to some extent, Masterman's (15) description of the nervous system of the *Actinotrocha*, especially since a shadow of doubt has been cast upon his work by some who have studied the *Actinotrocha*.

Partly because Species B. seems to be a much more highly developed *Actinotrocha* than Species A., and partly because of its similarity to the one that Masterman studied (which is of so much theoretical interest), we shall confine the description and figures to the nervous system of Species B., although we are convinced that this *Actinotrocha* is not that of *Phoronis architecta*, but of an adult that has not been discovered.

We must admit that we have been very unsuccessful in the attempt to study the nervous system of the *Actinotrocha* by means of methylene blue and ammonium molybdate. Gold chloride has given no better results than staining with iron haematoxylin.

If the dorsal surface of the hood of a live *Actinotrocha* Species B. be examined, one will find that there are a great many fibres which run in more or less definite tracts (fig. 36). Many of these fibres have nuclei along their course and are undoubtedly muscle fibres, while others run to the edge of the hood and there seem to be continuations of certain cell-like bodies which Ikeda was the first to describe (fig. 37). Although we have seen these bodies on all occasions in surface views stained with methylene blue, yet in sections we have never been able to make them out, if they are nerve cells. It must be mentioned, however, that in transverse sections through the edge of the hood every 3 μ section shows at least one nucleus closely applied to the ring of nervous tissue running round the edge of the hood (fig. 43). These occupy the same position with reference to the edge of the hood that the cell-like bodies do which are seen in surface views, but we take them to be the nuclei of muscle cells, and frequently we have traced deeply stained muscle fibres arising from them (fig. 43). Within the nervous tissue of the preoral ring we have found no structures which we could consider to be the cell-like bodies mentioned by Ikeda (9).

Ikeda has figured a great many fibres arising from the ganglion, but in the *Actinotrochæ* that we have examined we have not been able to see the connections; however, we do not wish to deny that they exist.

The three median nerves arising from the anterior side of the ganglion and running forward to the edge of the hood, and two longitudinal tracts of nerve fibres arising from the posterior side of the ganglion, can be easily made out, but the large majority of fibres which compose the broad tract shown in fig. 36 are not connected with the nerve ganglion. There are some individual differences in the arrangement of the above tracts, but in general they are about as shown in fig. 36.

On each side of the medio-dorsal line in the region of the youngest tentacles a tract of fibres can be seen running longitudinally. In the region where the edge of the preoral hood is inserted into the collar a small tract made up of a few fibres branches off from the dorsal longitudinal tract and passes into the edge of the preoral lobe. Somewhat farther forward each dorsal longitudinal trunk spreads out sometimes into three rather indefinite tracts, most of whose fibres seem to reach the edge of the hood. Many of the fibres of the anterior branch appear to end in the region at the sides of the ganglion, but no connection with the latter could be found.

Immediately posterior to the ganglion a tract of fibres (fig. 36) is seen which runs for a short distance transversely to the long axis of the *Actinotrocha*. On both sides the fibres of this tract soon diverge from one another and in this way distribute themselves over the anterior part of the hood, ending at the edge of the latter (fig. 36).

Masterman (15) has figured (Pl. XVIII, fig. 2) certain nerve tracts to the right and left of the three nerves arising from the anterior end of the ganglion and finds that these "run forward and outward and then bend backward and take a course to the posterior corner of the hood."

A lateral view of the hood of *Actinotrocha* Species B. shows sometimes fibres gathered together in trunks, but these never take the direction as shown by Masterman. They diverge rather regularly and end all along the edge of the hood instead of at the posterior corners of the same (fig. 37). They are in no way associated with the ganglion and do not have the appearance of being even when the hood is turned upward out of its usual position.

For several reasons we believe that the complicated tracts of fibres seen in a surface view of a live *Actinotrocha* Species B. are not nerve fibres but muscle fibres. First, many of them show along their course nuclei resembling nuclei of muscle cells. Second, cross sections through the hood show that there is a rather heavy lining of muscle fibres which run in the same general direction as do the fibres shown in the surface view. Third, there is no connection between these fibres and the nerve ganglion.

From the posterior side of the ganglion two tracts of nerve fibres pass out and can be traced backward some little distance, but they are soon lost to view, as Ikeda (9) has found to be the case when studying methylene-blue preparations.

Sections through *Actinotrocha* Species B. bring out quite plainly certain nervous tracts which appear as thickenings of the subepidermal nervous tissue and which correspond in a large part to the principal nerves described by Masterman.

Anterior to the ganglion a section through the hood shows the parallel nerves which run from the anterior side of the ganglion to the anterior edge of the hood. The boundary of these nerves, as shown in fig. 44, is a little too definite. The subepidermal nerve tissue, which forms a thin layer below the ectoderm cells, is not shown in the series of sections to be described.

Following the sections posteriorly we come to the ganglion, which in this specimen has become invaginated, together with the overlying epidermis, so as to form a pit. A cross section through this pit is shown in fig. 44*b*. The cavity of the pit is lined by epidermis, while peripherally the wall of the pit consists of the ganglion cells and the nerve fibres of the ganglion (figs. 38–44*b*). The nuclei of the ganglia are easily made out, but it is only after staining very deeply with iron hæmatoxylin that the cytoplasm can be seen. The invagination in the region of the ganglion is unusual and is brought about by the violent contraction of the hood when immersed in the fixing fluid. This undoubtedly is the same condition that Masterman (15) has described and the same structure that he has homologized to the "neuropore" of the *Chordata*, or that he has compared to the tubular dorsal nervous system of the same type as that of *Balanoglossus*. (Q. J., Vol. XL, page 295, 296.) It should be mentioned, however, that Masterman (16*b*) in his answer to Roule has admitted the error of his rather hasty conclusion.

Menon (17) has recently described a tubular nerve ganglion for a certain *Actinotrocha*, but the structure is probably due to fixation.

Immediately posterior to the ganglion a cross section shows two thickenings of the subepidermal nervous system. These thickenings are what Masterman has described as the dorsal longitudinal nerves and they can be traced from the ganglion. They are almost exactly between the dorsal muscle tract and the epidermis of the dorsal wall. A little farther back these so-called nerves are not quite as distinct, but when the region of the first pair of tentacles is reached they become more prominent again and diverge, passing down the lateral walls along the bases of the tentacles (fig. 41). They meet in the ventral region and thus form a ring-like thickening of the subepidermal nervous system, which is undoubtedly the same that Masterman has described as the "collar nerve ring" (fig. 42). Ganglion cells are demonstrable in this nerve ring by staining deeply with iron hæmatoxylin (fig. 39). As we shall show in the account of the muscular system there is a ring of muscle fibre which follows the nerve ring.

Masterman says that "fibers pass mid dorsally as a pair of tracts, giving off branches to the body wall and terminating in a nervous ring just anterior to the perianal band." In his figures of sections, however, the pair of tracts does not show back of the most dorsal pair of tentacles. In *Actinotrocha* Species B. there are no definite tracts of nerve fibres running longitudinally from the region where the collar nerve ring passes obliquely downward from the dorsal surface of the collar. Nerve fibres are undoubtedly present all along the dorsal wall, but these are not massed together in tracts and are simply the fibres of the ordinary subepidermal nervous tissue. The nervous ring in front of the perianal band is not present in the *Actinotrocha* that we have studied.

Masterman (15) finds that part of the nerve ring around the edge of the hood passes up to the nerve ganglion when it reaches the insertion of the hood, and that numerous fibres also appear to pass on to the ventral surface of the collar region. Live *Actinotrocha* (Species A. and Species B.), when examined under the microscope, do not show a branch of the nerve ring of the lobe passing upward to the nerve ganglion. Sections also fail to show this condition, which is very necessary to Masterman's comparison of the nervous system of *Balanoglossus* and the *Actinotrocha*. Fibres from the nerve ring do, however, pass on to the ventral surface of the collar region.

Numerous fibres, which Masterman speaks of as passing down on to the ventral collar wall, are massed in the *Actinotrocha* Species B. into two definite thickenings which are seen in fig. 44*c* and fig. 40. These thickenings of the nervous tissue gradually approach one another as we trace the sections backward and come to run along the same line as do the two ventral muscle tracts of the collar, but before the line of insertion of the ventral tentacles is reached these thickenings are lost in the subepidermal nervous tissue.

We have not been able to make out either in sections or in surface mounts any definite nervous tract running from the collar nerve ring along the ventral region of the trunk, although, as before said, there is a subepidermal network of nervous tissue throughout the wall. It will be remembered, however, that above we have described two longitudinal dorso-lateral tracts of muscle fibres, and there are quite numerous longitudinal muscle fibres in the ventral wall of the trunk. There is also a fairly well-developed layer of circular muscles, and these, together with the longitudinal muscles, give the appearance in surface views of the longitudinal tracts giving off branches.

The nervous system of the *Actinotrocha* of *Phoronis sabatieri* is less highly developed, judging from the specimens we have examined, than that of either Species A. or Species B. The ganglion, or, as Roule (20) calls it, the "plaque céphalique," contains ganglion cells like those we have found in other *Actinotrochæ*, which shows that there is something more present than a simple subepidermal nervous system, such as Roule has described, in the *Actinotrocha* of *Phoronis sabatieri*.

Muscular system.—There is no doubt but that there is some diversity in the arrangement of muscle fibres in the different species of *Actinotrochæ*. A study of the two species, A. and B., as well as the description of different species by other investigators, convinces us of this.

In the study of the muscular system the best results were with material fixed in Flemming's strong solution and stained with Haidenhain's iron hæmatoxylin. These solutions make the muscle fibres stand out very distinctly, whereas material fixed and stained with other fluids shows them so feebly that the muscle tracts might easily be overlooked.

Ikeda (9) has described a pair of bundles of muscle fibres springing from "the hind lateral corners of the ganglion and running divergently downward until they insert themselves in the collar walls between the first and second tentacles." These muscles, to which he has given the name of "retractors," are present in the *Actinotrochæ* Species A. and Species B. (figs. 34, 35, 45, 45*a*).

The "retractors" that Ikeda figures in the trunk cavity of one of the Japanese *Actinotrochæ* were not found in either *Actinotrocha* Species A. or Species B.

Another pair of bundles of muscle fibres is found in Species B. They spring from the wall of the hood at the sides of the ganglion, traverse the cavity of the hood and become inserted on its ventral wall directly under the ganglion (fig. 45*a*).

Certain tracts of muscle fibres are very highly developed in Species B. Transverse sections (stained with iron haematoxylin) through the wall of the hood in front of the ganglion show black dots spread over the internal dorsal surface of the hood, and these seem to be embedded in the mesodermal lining. These dots are the cut ends of muscle fibres, and as the sections are followed posteriorly, these dots gradually become massed about halfway between the ganglion and the sensory papilla and represent the sectioned ends of a pair of longitudinal muscle tracts which are bilaterally placed on the right and left of the median dorsal line (fig. 44). These two thick tracts of muscle fibres extend posteriorly in the dorso-lateral regions of the *Actinotrocha* and do not disappear until the perianal ring is reached. They are very characteristic structures in Species B. (figs. 44 to 44*h*), but we have not been able to make them out in Species A.

These muscle bands, no doubt, serve to draw the anal end of the body of the *Actinotrocha* up to the oral end during the metamorphosis. They are the most highly developed muscle tracts in the body of the *Actinotrocha* and their course is almost identical with the course of the "dorsal nerves" that Masterman describes.

Examination of cross sections of Species B. in the region of the vestibule shows the cut ends of numerous muscle fibres which are spread over the ventral surface of the collar. Passing

posteriorly, these fibres become massed into definite muscle tracts, about halfway back from the vestibule to the ventral insertion of collar-trunk mesentery (figs. 44*c*, 44*d*). These two ventral longitudinal tracts, which are bilaterally placed one on each side of the ventral median line, become separated, in most cases at least, from the ventral body wall in the region of the posterior pair of blood corpuscle masses and the latter become rather closely associated with them (fig. 46). We could not discover that these fibres were in any way related to the nephridia as has been described for some species.

In the region of the insertion of the ventral tentacles the muscle fibres of the ventral tracts become again applied to the ventral body wall, but definite tracts are no longer present. However, in the trunk region these fibres form a definite tract, which is confined to the ventral body wall, and it does not disappear until the perianal ring is reached (figs. 44 *g*, *h*, *i*).

Another tract of muscle fibres present in species B., which does not seem to be developed in other *Actinotrocha*, judging from existing descriptions, is that found in the region of the bases of the tentacles. From the dorsal muscle tracts, where the most dorsal and anterior pair of tentacles arises, muscle fibres are given off, which follow the bases of the tentacles and which form a well-developed ring of muscle fibres. In other words, there is a ring of muscle fibres which follows the line of insertion of the mesentery between the collar and trunk cavities (fig. 44*e*).

A tract of muscle fibres, which also seems to occur only in Species B., is one composed of only a few fibres, which are found running around the edge of the hood on the internal wall of the same (figs. 44 *a*, *b*). Where the edge of the hood passes into the wall of the collar cavity these fibres are seen to run on to the internal surface of the lateral wall of the collar and to mingle finally with the fibres of the dorsal tract. The direction these fibres take when they pass on to the wall of the collar reminds one very much of the fibres which Masterman (15) figured as nerve fibres.

On the internal ventral surface of the hood in both species of *Actinotrocha* there is a system of muscle fibres arranged concentrically. They run almost parallel with one another and with the edge of the hood (figs. 47 and 44*a*).

Beside the tracts of muscle fibres which have been described there are, lining the walls of the collar and trunk, circular muscle fibres lying between the longitudinal muscle fibres and the ectoderm. These have been generally observed by previous workers as have also the muscular covering of the ventral pouch and the muscle cells of the dorsal blood vessels.

Body cavities, mesenteries, etc.—Much difference of opinion exists as to the origin and limits of the body cavities in the *Actinotrocha* and also as to the value of these cavities in determining the phylogenetic history of *Phoronis*.

Roule (20) stands alone in considering the *Actinotrocha* to have but one body cavity, which is lined by an epithelium formed from mesenchymatous cells. He absolutely denies the presence of any mesenteries.

Through the kindness of Mr. Longchamps we have been able to study the *Actinotrocha* of *Phoronis sabatieri*, and have found that the mesentery between the collar and trunk is present, although it is less highly developed than in other species. We are unable, with the material at hand, to give any opinion as to the presence of a mesentery between the preoral lobe and collar cavities.

Caldwell (3) claims that there are but two body cavities, and that these are separated by a mesentery (collar-trunk mesentery of Masterman).

Longchamps (12) is inclined toward the view of Caldwell, while Ikeda (9) finds the mesentery dividing the lobe and collar, which, however, he says, is incomplete. Both of these investigators recognize the presence of the ventral mesentery.

Menon (17) finds three body cavities (preoral, collar, and trunk), a ventral mesentery, and indications of a dorsal mesentery in the trunk.

Masterman (16) considers that the *Actinotrocha* have five body cavities—an unpaired lobe cavity, a paired collar cavity, and a paired trunk cavity. This idea is based on his study of the

early development of the body cavities and not on the adult organization of the *Actinotrocha*, for in the collar he finds only a dorsal mesentery (no other investigator has seen this), and in the trunk only a ventral mesentery.

While it is possible that the mesoderm arises as diverticula from the enteron, as Caldwell and Masterman have described, yet Longchamps (12), who has recently reinvestigated the early embryology of the form that Caldwell worked on (*Phoronis kowalevskii*), denies the origin of the cavity in front of the collar trunk mesentery from enteric diverticula. Ikeda (9), who recognizes the "anterior diverticula" of Caldwell in the Japanese species, nevertheless holds that the body cavities do not arise from anterior diverticula, but are simply produced by mesoblast cells applying themselves to and forming the lining of the ectoblastic and entoblastic wall.

In the section on the mesoderm we have stated that in the embryo of *Phoronis architecta* we do not find that the mesoderm arises from enteric diverticula. There can not be the least doubt, however, that the preoral lobe at an early stage becomes lined by a sac of mesoderm cells and that the wall of this sac gives rise to the mesentery. Furthermore, this sac is extended postero-laterally into two horns which are characteristic of the cavity of the preoral lobe, according to Masterman, Ikeda, and Menon. It must be admitted, however, that this sac does not seem to retain its character as a sac, but that the cells become separated and apply themselves here and there to the walls of the preoral lobe. The mesentery remains intact and can not be considered as a secondary structure as has been suggested by Longchamps. Although we agree with Ikeda's statement that the mesentery between the lobe and the collar is incomplete laterally in the fully developed *Actinotrocha*, yet in the *Actinotrocha* of *Phoronis architecta*, at least, it must be considered as a definite mesentery.

The fully formed *Actinotrochæ* (Species A. and Species B.) do not show a complete epithelial lining to the preoral lobe, but the mesoderm cells are arranged as described in the young larva.

It is stated above in the part on the mesoderm that we do not find that the lining of the collar cavity is of enterocœlic origin in *Phoronis architecta*. However, in the fully formed *Actinotrocha* there is an undoubted mesodermic ephithelium lining the somatic wall. This layer is very conspicuous immediately before metamorphosis, because it becomes separated from the somatic wall prior to becoming transformed into the ring vessel of the adult (figs. 51*g*, 51*h*).

The splanchnic wall of the collar cavity in the *Actinotrochæ* that we have examined is devoid of a mesodermal lining, and the occurrence of mesoderm cells on the wall is very infrequent. This condition of affairs in the well-developed *Actinotrocha* is what one would expect from the disposition of the mesoderm cells in the very young larvæ of *Phoronis architecta*, where it is only very seldom that any are found on the stomach wall (fig. 24).

The absence of a mesodermal lining on the splanchnic wall of the collar cavity is made all the more evident by the examination of cross sections showing the collar-trunk mesentery (figs. 51*g*, 51*h*). When the mesentery reaches the stomach wall, instead of dividing into two layers, one of which would be continued into the mesodermal lining of the stomach wall of the collar cavity, it turns abruptly upon itself and becomes the lining of the stomach wall of the trunk. We have never found the least indication in the collar cavity of a dorsal mesentery such as Masterman (15) has described in the *Actinotrocha* from St. Andrews Bay. The trunk cavity is lined throughout by a sac of mesodermal epithelium, and the mesentery is plainly seen to be continuous with the lining of the somatic wall and with the lining of the wall of the gut. The ventral mesentery of the trunk is present in Species A. and Species B., and while there is no dorsal mesentery we have found indications of it in two specimens only (Species B.) at the posterior end of the trunk. We can not say, however, that it has any ontogenetic significance (figs. 48, 44*i*, 44*g*). We have also found the ventral mesentery to be present in the *Actinotrocha* of *Phoronis sabatieri*.

The ventral pouch fills a large part of the trunk cavity in the fully formed *Actinotrocha*, and just before metamorphosis it frequently pushes the collar trunk mesentery well forward into the collar cavity, thus making the study of the relation of the different parts quite difficult. Both

the external opening of the ventral pouch and the nephridial openings are found on the ventral wall of the trunk just posterior to the insertion of the mesentery as in other species.

Nephridia.—Wagener (23) was the first to observe the "nephridial bouquets," but Caldwell (3) was the first to publish a careful study of the nephridia of the *Actinotrocha*. Goodrich[a] (6) has recently published a paper on the excretory organs of *Amphioxus*, and he adds a note on the nephridium of the *Actinotrocha* which confirms Caldwell's view. The two latter investigators agree that the nephridium ends blindly without funnels; that there are tubular processes, each one containing a lumen and tipped with an excretory cell, and that these processes radiate out from the blind inner end of the nephridial canal.

Longchamps (12) is inclined to accept Caldwell's view of the subject. Roule (20) and Ikeda (9) seem to hold the view that the nephridial canal ends blindly without branching, and that the blind end is tipped with excretory cells, which, however, are not perforate.

Masterman (15) and Menon (17) have another view. They both think that the nephridial canal terminates internally as two (Menon) or more (Masterman) funnels, and they recognize the existence of long processes without lumens attached to the ends of the funnel.

We have not been able to make a study of the nephridia of the living *Actinotrocha*, but we have investigated them by means of sections in Species A. and Species B. For this purpose we have used material fixed in Flemming's fluid and also in corrosive acetic. The sections were stained with iron haematoxylin. Our work has been done with very high powers (Zeiss obj. $\frac{1}{12}$ and No. 12 Zeiss compensating occulare).

The nephridia of the two *Actinotrochæ* have much the same structure, but in Species A. we have been unable to find that the internal end of the nephridial canal branches, while in Species B. the internal end divides into two short branches.

Figs. 52, 52*a*, 52*b* represent three transverse sections through the anterior part of the nephridium of Species B. Fig. 52 is through the nephridial canal just posterior to its internal end. Darkly staining dots seen in the lumen represent cross sections of long flagella such as Goodrich (6) has described in the "solenocytes" of *Amphioxus*.

Fig. 52*a* shows a section through the nephridial canal a few sections anterior to that of fig. 52, and at the same time it shows the lower or most posterior branch with a few excretory cells and their processes.

In fig. 52*b*, which is a section through the tip of the upper or anterior branch of the nephridium, the lumen of the nephridial canal is reduced to a very small clear space.

If a section is taken in a longitudinal direction through the nephridial canal and its excretory processes (fig. 52*g*), it is seen that the distinct walls of the nephridial canal disappear when the "bouquet" of excretory cells is reached, but that the end is blind and that it is merely a thin walled bulb from whose surface radiate the processes of the excretory cells. The structure of these processes is the same in both species that we have examined except that in Species A. they are much shorter, which might account for the different descriptions we find in the literature. We are convinced that in both species the excretory processes contain lumens, that these lumens are continuous with the lumen of the nephridial canal, and that they contain flagella.

Each of the excretory processes is tipped by a body the distal end of which is drawn out into a sharp-pointed process. The outline of only one cell could be seen in the body. Sometimes it contains but one nucleus, which may be oval in shape or bent almost at right angles (fig. 52*d*), but in the majority of cases there are undoubtedly two nuclei (fig. 52*e*). Fig. 52*c* shows a cross section through one of these bodies. If a transverse section of the nephridial processes is taken (fig. 52*f*), it is seen that each has a definite wall and that inside there is a definite dot which we take to be a cross section through the flagellum. This flagellum has its origin from the cell body at the end of the process, and the indications are that the flagellum extends throughout the length of the process into the lumen of the nephridial tube.

[a] Since writing this paper a description of the nephridia of the *Actinotrocha* by Goodrich (6*a*) has come to our notice. Our account agrees to a large extent with his.

We are not prepared to say that the cell bodies at the end of the excretory processes are composed of two cells, but it is a fact that two nuclei exist, and this conclusion is not based on sections through bent nuclei which might lead one to think that there were two when only one existed. It will be seen from this description that the anatomy of the excretory cells and processes of the *Actinotrochæ* which we have studied resembles that of similar structures described by Goodrich for *Amphioxus*.

There is nothing new to add concerning the nephridial canal except that a longitudinal section through it, which has been stained with iron hæmatoxylin, shows long flagella extending some distance from the distal end into its lumen (fig. 52*g*).

Sections of the *Actinotrocha* of *Phoronis sabatieri* show that the nephridia resemble those of other *Actinotrochæ* studied, although they do not seem to be as well developed as those of Species A. and B. The specimens at hand show that the internal opening in the collar cavity is situated at about the same level as in other *Actinotrochæ* and not at the level of the œsophagus, as Roule (20) has indicated.

The course which the canal takes is like that which has been described by other investigators, and we agree with the observation of others in regard to the nephridial canal opening to the exterior at the sides of the ventral pouch opening.

Masterman (15) describes a pair of ciliated pores opening to the exterior on the dorsal surface of the preoral lobe. These, he finds, lead into tubes closely similar in cross section to the cross section of canals of the collar nephridia, and these tubes have an internal opening into the preoral lobe cavity. He compares the external pores to the proboscis pores of *Cephalodiscus*. In the Zoologisher Anzeiger, 1901, Volume XXIV, page 231, he admits that their occurrence is variable. No other investigators have found these organs. Ikeda mentions the fact that flask-shaped glands on the upper face of the preoral lobe occur in one larva studied by him, but he denies that they are such organs as Masterman describes.

Masterman (15) also finds thin-walled organs lying in the hæmocœle space immediately below the anal ciliated band. Speaking of these (15) he says: "A pair of organs which I have not fully made out, but they may be the rudiments of the trunk nephridia." Masterman, however, denies their existence in a later paper, and no one else has seen the organs, as far as we know.

Rudiments of the adult blood vessels in the Actinotrocha.—Many investigators of the *Actinotrocha* have recognized the beginnings of the adult blood vessels, but E. B. Wilson (24) is the first one who clearly states the fact that the cavity containing the blood corpuscle masses gives rise to the ring vessel of the adult, although Metschnikoff seems to have had some such idea. Caldwell (3) and Ikeda (9) confirm the statement of Wilson with reference to the origin of the ring vessel of the adult.

While Masterman (15) describes a much more complicated vascular system for the *Actinotrocha* from St. Andrews Bay than that of all the *Actinotrochæ* examined, yet we agree with him in his view that the cavities of the blood vessels may be considered as vestiges of the segmentation cavity.

Above we have given our opinion that the "subneural sinus" (Masterman) does not exist in the *Actinotrochæ* that we have examined, and that although there is a space beneath the ganglion it has no connection with the dorsal blood vessel.

The blood vessels of the adult are represented in the *Actinotrochæ* Species A. and B. by a dorsal vessel (figs. 34, 35) extending along the median dorsal line of the intestine, from the mesentery between the collar and trunk almost to the posterior end of the stomach, where there are small cæcal outpushings of the splanchnic mesodermal walls of the end of the stomach. This dorsal blood vessel, although it is a completely formed vessel, has arisen from a proliferation of the cells of the splanchnic mesodermal wall along the dorsal median line of the stomach, and its lumen is really a part of the blastocœle—i. e., it is a part of the space between the splanchnic mesodermal lining and the wall of the stomach. Posteriorly, the dorsal blood vessel becomes indefinite and passes into the ordinary splanchnic mesodermal lining, thus really being open posteriorly into the space between the wall of the stomach and the mesodermal lining.

At the time of metamorphosis in the *Actinotrochæ* Species A. and Species B., there is no sign of a ventral blood vessel along the stomach, such as Masterman (15) and Roule (20) describe.

We have been unable to find the "ring sinus" which, according to Masterman, connects the dorsal vessel with the ventral vessel at the end of the stomach, nor have we seen the "postoral ring sinus" connecting the dorsal vessel with the ventral vessel.

Masterman's "postoral ring sinus," "ventral blood vessel," and "ring sinus" (situated at the junction between the stomach and intestine) will be discussed in the section on the metamorphosis.

There is undoubtedly a space between the wall of the perianal ring and its mesodermal lining (fig. 49) in preserved specimens which seems to be what Masterman calls the "haemal ring," but it does not become any organ of the adult.

As stated above, we believe with Wilson, Caldwell, and Ikeda that the cavity of the collar and its somatic mesodermal lining become the ring vessel of the adult.

We shall continue the discussion of the further development of the dorsal blood vessel into the efferent and afferent vessels of the adult in the section on the metamorphosis.

Masterman speaks of haemal sinuses passing down the tentacles, but says that they are not very decided. Ikeda has, however, investigated these structures carefully, and we thoroughly agree with his view that the cavity of the collar, together with its somatic lining, extends into the tentacles, and that these prolongations become the tentacular vessels of the adult. This condition is shown very plainly in a dorso-lateral section of the *Actinotrocha* Species A. (fig. 50).

Blood corpuscles and their origin.—E. B. Wilson (24) has touched upon the origin of the blood corpuscles, and according to him they develop in solid masses adhering to the stomach walls near the base of the tentacles. Caldwell (3) finds that the corpuscle masses "arise from the mesoblast cells in front of the septum," but he has nothing further to say about their position or origin. Ikeda (9) describes the blood corpuscles as arising from "gigantic mesoblast cells in the body cavity of the larvæ with one or two pairs of tentacles." Since the publication of this paper, Ikeda has rejected this view, although he has published nothing on the subject. Menon (17) thinks that the blood corpuscles arise from the splanchnopleure covering the stomach and its diverticulum. According to Cori (4), the blood corpuscles in the adult are formed from the endothelium of the blood vessels.

In the *Actinotrocha* Species A. (probably that of *Phoronis architecta*) the blood corpuscles usually make their appearance during the 14-tentacle stage, as in "Type A" described by Ikeda, although we have found larvæ of this stage in which definite blood corpuscles were not present.

Actinotrocha Species A. with 16 tentacles invariably has blood corpuscles, and they are present in the so-called collar cavity as two masses more or less closely applied to the ventro-lateral walls of the stomach (figs. 51 *g*, *h*). In some cases, however, they are separated from the wall by a considerable space.

The transverse section of a larva with 12 tentacles in a plane just posterior to the base of the tentacles, but anterior to the mesentery, always shows two masses of cells bilaterally placed and closely applied to the mesoderm lining the ventro-lateral somatic wall (fig. 53). Occasionally cells are found in these masses, situated very close to the mesodermal lining, which are decidedly spindle-shaped in form and whose nuclei resemble those of the cells of the mesodermal lining, both in shape, size, and internal structure. These cells are not very rich in cytoplasm. Most of the cells, however, are almost three times the size of the cells lining the somatic wall, the cytoplasmic part of the cell having increased in size to a greater extent than the nucleus. Most of the nuclei have large deeply staining nucleoli (fig. 54).

In some specimens parts of these masses of cells are apparently in the act of wandering across the body cavity to the position the blood-corpuscle masses occupy in the fully formed *Actinotrocha*.

Some 15 or 20 larvæ with 12 or 14 tentacles have been sectioned, and with one exception we have found that when the mesodermal masses are present on the ventral body wall there are no blood-corpuscle masses present in the larva, and that when the blood-corpuscle masses are

present there are no mesodermal masses. In this exception small blood-corpuscle masses were found applied to the stomach wall, and masses of cells bilaterally placed were found on the ventral somatic wall, but these cells had already taken on the character of blood corpuscles.

Ikeda (9) has described a "mesoblastic cell mass" which he evidently considers as giving rise to the adult body cavity, and its position is very similar to that of the mesoblastic masses described above. They are both products of the mesoblastic lining of the ventral somatic wall and are situated between the plane of the bases of the tentacles and the plane of the somatic insertion of the mesentery between the collar and trunk. Although Ikeda does not touch upon the very early origin of the adult body cavity, yet it seems probable that he considers it as arising from a single mass of cells. The mesoblastic masses described above are paired and bilaterally placed, and they are present only in the young larva of 12 or 14 tentacles. Furthermore, in the larva with 12 or 14 tentacles there is no sign of the beginning of the adult body cavity. Althoagh these mesodermal masses which, according to our observations, give rise to the blood corpuscles have a similar position to the fundament of the young adult body cavity, yet we are convinced that they do not give rise to it.

In Species A, there is no intimate relation between the masses of blood corpuscles and the nephridia, such as has been described by Masterman (15) for the species from St. Andrews Bay, and by Longchamps (12) for *Actinotrocha branchiata*. In the larva of 16 tentacles the blood-corpuscle masses are, however, closely applied to the stomach wall in the region of the digestive area. There is no mesodermal epithelium covering that part of the surface of the stomach which lies within the collar cavity, and the blood corpuscles seem to be so intimately related to the digestive areas that we are inclined to believe that they receive nourishment from them.

While the blood corpuscles vary in size and undoubtedly multiply by karyokinetic division, yet we have never found the "large and somewhat coarsely granular" and the "smaller finely granular" corpuscles that Ikeda (9) speaks of, nor in this species have we found any "gigantic mesoderm cells" in the region of the blood-corpuscle masses. Very large cells in close relation to the blood corpuscle masses are found in some specimens of *Actinotrocha* Species B. (fig. 44*f*). These cells resemble the cells described in the old gastrula of Species A. as arising from the wall of the archenteron, only they are not as coarsely granular as the latter. While in *Actinotrocha* Species B. the cells are found in most cases closely associated with the blood corpuscles, we have never seen them in the process of division and do not believe that they give rise to blood corpuscles. Their occurrence is quite variable, but as far as has been observed they are not present in the *Actinotrocha* which are ready to metamorphose. They are not phagocytes, nor are they pigment cells, and the only name which we feel justified in giving them is large free mesoderm cells. Frequently they are also found in the posterior end of the trunk cavity (fig. 44*i*).

Roule (20) holds that the nephridia end internally at the level of the œsophagus, and he shows this in a figure. We have made cross sections through this region and have found masses of cells in much the same place as Roule has shown. These cells seem to be blood corpuscles, but very few specimens have been examined, and only one of these showed these masses of cells.

Rudiment of the "adult collar cavity" (Ikeda).—Ikeda has observed a mesodermal cell mass on the ventral somatic wall just under the second tentacle in rather young specimens of all the Japanese *Actinotrocha*. He has traced the development of this mass of cells and finds that a cavity arises in it which, before metamorphosis, becomes quite spacious and extends into the tentacles. We are able to confirm Ikeda's view that this cavity is the rudiment of the "adult collar cavity," or "supraseptal cavity" of the adult, as it is usually called (figs. 50, 48, 51*h*, 45*b*, 46).

METAMORPHOSIS.

Several investigators have carefully described the external characteristics of the metamorphosis of the *Actinotrocha*, so it is unnecessary to enter into a detailed description.

Wilson (24) studied the metamorphosis of *Actinotrocha* Species A. and Species B., which are found in Chesapeake Bay, but he did not cut sections of his material. Ikeda (9), however, has investigated the internal changes which take place during metamorphosis and has added a val-

uable contribution to the subject. The behavior during metamorphosis of *Actinotrochæ* Species A. and Species B. from Beaufort Harbor seems to be quite the same as that of the two *Actinotrocha* which Wilson has observed, and there is little doubt but that they are of the same species.

As Wilson has stated, the metamorphosis of *Actinotrocha* Species A. (fig. 34) takes place much more quickly than that of Species B. (fig. 35). In fact, we have never obtained a completely metamorphosed specimen of the latter, although many times we have found specimens of this species with the ventral pouch well evaginated (fig. 55). We have tried to make the conditions favorable for the completion of the metamorphosis by covering the bottom of the aquarium with a layer of sand rich in diatoms and also by changing the water frequently. Under these conditions the larvæ (Species B.) would invariably sink to the bottom and move around on the sand apparently in search of a favorable place to finish the metamorphosis. The latter never occurred, however, although sometimes the larvæ would attach the end of the ventral pouch to the bottom of the dish. In this way the creature would often remain for days and although the preoral lobe and larval tentacles would degenerate the anal end of the larva would never become turned upward so as to lie in close proximity to the mouth.

As we have said before, we are inclined to think that the *Actinotrocha* Species B. belongs to an adult which lives under different conditions from that of *Phoronis architecta*, and we should not be surprised if it were found to be the *Actinotrocha* of a deep-water form. Although *Cerianthus* occurs in Beaufort Harbor, we have never found *Phoronis australis* associated with it.

Actinotrocha Species A., as a rule, metamorphoses in about twenty minutes (figs. 56, 56*a*, 56*b*), and usually just before this takes place it sinks to the bottom of the dish, but occasionally metamorphosis occurs on the vertical side of the dish near the surface of the water, the young *Phoronis* remaining fixed where the metamorphosis takes place.

Preoral lobe and tentacles.—Usually the larval or distal part of the tentacles (Species A.) and the preoral lobe are swallowed during metamorphosis. The proximal parts of the tentacles become directed upward and constitute the tentacles of the adult. They always number 18 in the very young *Phoronis* (Species A.) and there is an indication of the horseshoe arrangement which is found in the adult (fig. 56*b*).

The preoral lobe does not give rise to the epistome of the adult, for as Menon (17) has correctly observed, this structure is not present in the very young *Phoronis*. However, the epistome, which is of ectodermal origin, soon makes its appearance, and when the creature has 30 tentacles it is a very conspicuous organ (fig. 57).

Ganglion.—The ganglion on the dorsal surface of the hood is lost when the preoral lobe is swallowed, and hence does not give rise to the so-called brain ganglion of the adult.

Ectodermal wall of collar.—Although the preoral lobe degenerates, the wall of the collar does not, but becomes drawn inside the body of the young *Phoronis* and forms the wall of the oral end of the gut.

Perianal ciliated ring and ectodermal wall of the trunk.—When the critical point in the metamorphosis is reached—that is, when the posterior end becomes drawn up to the region of the mouth—the perianal ciliated ring is usually seen as a protuberance in that region (Wilson's fig. 12), but shortly after this it becomes drawn in, and, together with some of the ectoderm, becomes the lining of that part of the rectum which is near the anal opening. The drawing in takes place to such an extent that most of the ectodermal wall of the trunk of the *Actinotrocha* becomes incorporated in the wall of the rectum, as Caldwell has observed.

This process, together with the drawing in of the ectodermal wall of the collar to form the wall of the oral end of the gut, seems to cause a change in the position of the nephridial canals. (See section on nephridia.)

Cavity of the preoral lobe.—Since the preoral lobe is lost during the metamorphosis, its cavity does not take part in the structure of the adult.

Mesentery between the lobe and collar.—This mesentery does not persist.

Larval collar cavity.—As has been stated by other investigators, and as we have observed, the larval collar cavity with its mesodermal wall becomes the ring vessel of the adult. This organ will be discussed further in the section on the vascular system.

"*Adult collar cavity*" (Ikeda).—This cavity, which is found in the well-developed *Actinotrocha*, undoubtedly becomes the "adult collar cavity" or supraseptal cavity of the adult, as Ikeda says. In the young *Phoronis* it is seen as a cavity which occupies all the region anterior to the transverse septum and which is prolonged into the tentacles. It is lined by a mesodermal epithelium and contains the ring vessel with its tentacular vessel.

Trunk cavity and cavity of the ventral pouch.—These cavities become the infraseptal cavity of the adult.

Ventral mesentery.—The ventral mesentery of the *Actinotrocha* no doubt becomes the mesentery in the adult which Cori calls the "hauptmesenterium" and which Benham names the "œsophageal" and "rectal" mesenteries. Mesenteries are present in the very young *Phoronis* (just after the completion of the metamorphosis), which are found in the exact position that one would expect the ventral mesentery of the *Actinotrocha* to assume after metamorphosis. Ikeda's figures indicate that he considers the longitudinal mesenteries of the very young *Phoronis* to be the same as the ventral mesentery of the *Actinotrocha*, for he gives them the same name.

We can not offer any observation on the origin of the lateral mesenteries of the adult except that they are not present in the very young *Phoronis* that we have examined. They undoubtedly arise later in the life history.

Stomach diverticula.—This structure is not present in the *Actinotrocha* Species A., so we are not able to give any information on the subject. It seems to be the general opinion among those who have studied the metamorphosis that it does not persist as an organ in the adult.

Digestive areas.—While these organs persist for some little time after metamorphosis, they are not evident as organs in the adult *Phoronis architecta.*

Nephridia.—Caldwell (3), Ikeda (9), Longchamps (12), and Menon (17) have all observed the change in position of the larval nephridial canals which is due to the changes taking place during the critical period of the metamorphosis, and it is a quite well-established fact that the external ends of the larval nephridial canals come to be situated near the anal opening.

Just after the critical period a cross section through the anterior end of the young *Phoronis* cuts the transverse septum ("diaphragm," "collar trunk mesentery"), which runs obliquely and passes through the supraseptal and infraseptal cavities. It shows a transverse section through the nephridial canals, which are still attached to the mesentery, as in the *Actinotrocha*. Following the sections anteriorly, the canals are seen to open into the supraseptal cavity ("larval collar cavities," "ring vessel of the adult"), and they are still found in possession of their excretory cells. Posteriorly the sections show that the nephridial canals leave the septum and pass between the wall and the mesodermal lining of the infraseptal cavity (fig. 59). At this time their external openings are situated on the lateral epidermal wall in a transverse plane which is somewhat below the transverse plane of the anus, and they are by no means as near to the latter as they are in the adult *Phoronis*. It is seen from this description that during the critical period there is very little change in the structure of the larval nephridia or in their position, although the evagination of the ventral pouch and the drawing in of the ectoderm of the trunk to form the end of the rectum causes the anus to become rather closely approximated to the external nephridial openings.

Caldwell (3) says that the whole of the larval nephridial canals remains as the paired nephridia of the adult, while Ikeda thinks it probable that only the parts of the nephridial canals lying in the wall of the trunk persist. He assumes that the nephridial funnels of the adult, which both open into the infraseptal cavity, are secondary outgrowths of the above remnants of the nephridial canals.

As the metamorphosis continues, sections show that the excretory cells and that part of the nephridial canals situated in the larval body cavity have become obliterated, together with the portion of the nephridial canals running in the septum. While we do not wish to deny that the remnants of the nephridial canals and their external openings, situated originally in the trunk cavity of the *Actinotrocha*, become part of the nephridia of the adult, yet in the stage under consideration they could not be found. So far as we know, Ikeda is the only investigator who has given us figures illustrating the relation between the larval nephridia and the nephridia of the adult. While his fig. 64*c* shows the larval nephridial canals, his fig. 66, which is a cross

section through the anterior end of a young *Phoronis* and which shows a section through the young nephridium of the adult, does not prove that he is dealing with the same structure.

Vascular system.—It will be remembered that the vascular system of the fully developed *Actinotrocha* Species A. consisted of a dorsal blood vessel (figs. 51 *f, g, h*) running along the median line of the stomach from the dorsal insertion of the mesentery, between the collar and trunk, to the posterior end of the stomach, its lumen being a part of the segmentation cavity; a bunch of blood caeca formed at the posterior end of the stomach as evaginations of its splanchnic mesodermal covering and a loose sac of mesodermal tissue arising on the somatic wall of the collar segment and inclosing the larval collar cavity (figs. 50, 51 *f, g, h*). (See below for discussion of the "post-oral ring sinus," ventral vessel and the "ring sinus" at the junction of the stomach and intestine.)

There are several important points in the vascular system of the *Actinotrocha* which must be taken into account in order to understand its metamorphosis into the vascular system of the young *Phoronis*. First, that the dorsal blood vessel, which is formed from the splanchnic mesodermal lining of the trunk cavity, incloses a part of the space between the lining and the wall of the alimentary canal—i. e., the segmentation cavity—second, that this vessel dwindles away posteriorly and opens into the space between the lining and the wall of the alimentary canal; third, that the wall of the stomach in the collar segment is practically free from mesodermal lining (figs. 51 *g, h*), and that the larval collar cavity, with its somatic mesodermal lining, is a blood sinus; fourth, that the larval collar cavity is a part of the segmentation cavity; and, fifth, that during metamorphosis the act of drawing the stomach and intestine into the cavity of the ventral pouch causes pressure to be exerted on the larval collar cavity.

When the critical stage is being passed through, the blood-corpuscle masses break up and they are driven by the pressure on the collar cavity to the points of least resistance. As a rule some of the blood corpuscles are squeezed up into the dorsal region of the collar cavity where the dorsal blood vessel ends, and invariably some of the blood corpuscles pass from the larval collar cavity into the cavity between the wall of the alimentary canal and its mesodermal covering. In fact, as soon as the critical stage occurs, the splanchnic mesodermal lining in all regions becomes separated from the wall of the alimentary canal and thus allows the blood corpuscles to move about between these two layers throughout the extent of the alimentary canal.

The dorsal blood vessel ("mediangefäsz" (Cori), "afferent vessel" (Benham), and the ring vessel with its tentacular vessel are completely formed structures at this stage. The dorsal vessel is still freely open posteriorly into the space or sinus between the stomach wall and its mesodermal covering and blood corpuscles are carried back and forth from it to the sinus by the contraction and expansion of the former. Anteriorly the dorsal vessel can plainly be seen opening into the ring vessel (larval collar cavity.)

The origin of the connection between the dorsal vessel and the ring vessel and the manner in which the blood corpuscles find their way into the former are questions which have not been very satisfactorily elucidated. *Actinotrocha* Species A., does not present any great difficulties in the way of understanding how these processes take place. The dorsal blood vessel opens posteriorly into the sac-like sinus around the loop of the alimentary canal, and it seems probable from an examination of sections of the critical stage that it is also open anteriorly. Assuming that such is the condition, it will open into the space between the mesodermal lining and the wall of the gut. This space, however, is in free communication with the larval collar cavity (adult ring vessel) which contains the blood corpuscles. Under these conditions the blood corpuscles can pass into the dorsal blood vessel from either end.

Masterman (15) and Roule (20) both describe a vessel on the ventral stomach wall of the *Actinotrocha*. We have not found this vessel in the *Actinotrocha*, nor do we find it in sections of the critical stage.

At this time there is but one ring vessel in the supraseptal cavity, but we consider that it represents both the receiving and distributing vessels of the adult *Phoronis*.

Shortly after the critical point in the metamorphosis, the mesodermal lining on the left side of the oral limb of the U-shaped alimentary canal begins to show indications of becoming a blood

vessel, and when the metamorphosis is completed a definite vessel is seen, which opens posteriorly into the spacious blood sinus around the loop of the alimentary canal. Anteriorly before reaching the transverse septum, it divides into two branches, which run obliquely upward along the sides of the alimentary canal, almost encircling the same; these finally open into the ring vessel of the supraseptal cavity (fig. 60). The vessel described becomes the efferent vessel of the adult (figs. 78, 77, 75, 66) and its branches become part of the recipient vessel.

As Ikeda has pointed out, the efferent vessel of the adult corresponds to the ventral vessel which Masterman (15) and Roule (20) have found in the *Actinotrocha* before metamorphosis.

In all the completely metamorphosed *Actinotrochæ* that have been sectioned there is but one ring vessel, but the young *Phoronis*, when it is 12 hours old, possesses both the recipient and distributing vessels; these vessels, we believe, arise from the single ring vessel of the metamorphosing *Actinotrocha* by the fusion of its walls and by the subsequent separation of the two parts along the line of fusion.

Masterman, in his description of the blood system of the *Actinotrocha*, speaks of a "ring sinus" at the anterior end of the intestine which connects the dorsal and ventral vessels. He also says that there are two lateral branches of the dorsal vessel in the region of the pharynx which pass downward around the oesophagus ("post-oral ring sinus") and become continuous with the ventral vessel.

The former undoubtedly represents the sinus surrounding the loop of the alimentary canal in the young *Phoronis*, while the latter, no doubt represents the branches of the efferent vessel which become part of the recipient vessel of the adult. Masterman says that these branches open into the dorsal blood vessel, but such is not the case in the completely metamorphosed *Actinotrocha*.

From a comparison of Masterman's description of the vascular system of the *Actinotrocha* and Ikeda's and our own description of the same before and after metamorphosis, it is seen at once that this system develops more precociously in the form that Masterman studied. This condition, together with the facts that the lumen of the blood vessels are parts of spaces between the wall of the gut and its mesodermal lining and that the mesodermal lining of the alimentary canal fits loosely while the blood system is developing, gives additional weight to Masterman's statement that the dorsal vessel opens into the so-called "subneural sinus." However, in the *Actinotrochæ* that we have examined such a connection does not exist, and, as stated above, a "subneural sinus" or cavity caused by a lack of contiguity between the mesodermal wall of the preoral lobe and that of the collar cavity is not present.

THE ADULT PHORONIS ARCHITECTA.

Phoronis architecta was discovered by Andrews (1) in June, 1885, at Beaufort, N. C., and he described it as a new species, giving it the specific name "architecta," on account, no doubt, of its building a beautiful, straight tube. He finds that the tubes are made up of a clear, firm, chitin-like membrane covered with small, clear grains of sand, and he thinks that these grains are selected by the animal. Specimens collected from different localities in Beaufort Harbor vary considerably in regard to the character of the sand grains and quite often small fragments of dark shells are found mixed in with the latter. Occasionally two tubes occur cemented together; but this condition is rare, for they are usually isolated and embedded perpendicularly in the sand. When the specimens are brought into the laboratory and put into aquaria with sand and water, they usually crawl out of their tubes and begin to form new ones. Longchamps (13) has lately pointed out that the tube is formed by a secretion from the posterior end of the animal and not from the anterior end, as Cori has said. This is the case for *P. architecta*.

Above it is stated that the tubes are straight, but where new tubes are formed in the aquaria they are always twisted to a considerable extent, and they are attached firmly to the bottom of the jar. In its natural habitat, *Phoronis architecta* does not have a firm substratum to which to cement its tube, but it is seen from the above observation that when a solid surface presents itself, the tube may take on the condition found in some of the other species of *Phoronis* which are attached to rocks and shells.

Phoronis architecta lives at about low-water mark on the sand shoals, which are very numerous in Beaufort Harbor, and, as a rule, the individuals occur in patches. Three or four hundred specimens are often found within a radius of 4 or 5 feet, but one is very apt to find isolated specimens while digging in the sand anywhere in the harbor.

Only rarely do the tubes project above the surface of the sand as Andrews (1) has described, and in these cases the condition was due to disturbances of the surface of the sand, such as hollows made by *Callinectes*. Usually the upper end of the tube is from 3 to 5 cm. below the surface of the sand.

The average length of these tubes is 13 cm., and the average width a little over 1 mm. The adult when removed from its tube is about 1 mm. in diameter in the posterior one-third, and slightly less in the anterior two-thirds (fig. 61). The length of specimens taken out of the tubes varies with the amount of contraction from 20 to 25 mm., which figures are considerably lower than the length given by Andrews (about 50 mm.). The specimens which Andrews described must have been considerably more extended than any we have preserved. When the animal is in its natural habitat and undisturbed, however, it is capable of great extension, stretching the whole length of the tube and even considerably farther, so that its lophophoral end may project above the surface of the sand and reach for some considerable distance along its surface. We have not been able to preserve specimens in their extended condition, and they usually contract to from 20 to 25 mm. in length.

The anterior two-thirds of the living specimen has a flesh color, while the posterior one-third is dark-yellowish red and quite opaque, which is due to the fact that the gonads and blood caeca are situated in this region. In preserved specimens, the body wall is annulated (fig. 61), but such is not the case probably in the fully extended individual.

The crown of tentacles is quite simple compared to the crown of tentacles in *P. australis*, *P. buskii*, and *P. pacifica*. A cross section shows that it is crescentric and that the ends are not spirally coiled (figs. 62, 63, 64).

Andrews (1) has given us a description of the principal points in the anatomy of *Phoronis architecta*, which he has undoubtedly made brief because of the resemblance to the anatomy of *Phoronis australis* as described by Benham (2). In general our observations agree with those of Andrews, but there are a few points which merit discussion.

Lophophoral organs.—These peculiar organs (fig. 62) have been observed in several different species of *Phoronis*, and although functions for them have been suggested, the observations do not seem to have extended over a long enough period in the adult life of the worm to warrant a definite statement as to their function.

The lophophoral organs (fig. 62) lie one on each side of the median line within the concavity of the lophophore. They are outgrowths from the base of the inner row of tentacles, and, in some species at least, are quite conspicuous organs, but they do not arise until the *Phoronis* has reached its adult size. Organs located in the above region have been described for eight species, but the size and shape do not seem to be the same in all. Whether these differences are specific or whether the observations have been made at different periods in the adult life it is hard to say. Lophophoral organs like those present in *Phoronis architecta* are found in *P. psammophila*, *P. pacifica*, *P. mülleri*, and, no doubt, in some other species also. It seems, however, probable from the description of the anatomy of *P. buskii* and *P. australis* that in these species the lophophoral organs are much less highly developed than in the smaller species with fewer coils in the lophophoral crown. We have examined several specimens of *P. australis* with and without genital products, but in no case have we seen organs such as are present in *P. architecta*.

Various functions have been assigned to the lophophoral organs. McIntosh (14), working with *P. buskii*, considers that they are sensory in function, while Masterman (16), who has studied the same species, says that they are glandular and that they give rise to mucus which serves to hold the embryos together in masses. In other words, he considers them to be "subsidiary reproductive organs." Benham (2), who worked on *P. australis*, and Cori (4), who investigated *P. psammophila*, both give these organs a glandular function, while Andrews (1) thinks that

in *P. architecta* they are used in building the tubes. H. B. Torrey (22) has made the interesting observation that in some specimens of *P. pacifica* the lophophoral organs are like those in *P. australis*, while in others they are like those in *P. architecta*. It is probable that in part of the specimens which Torrey examined the lophophoral organs were not full grown, while in the rest they had reached their full development.

Our observations indicate that Andrews' supposition concerning the tube-building function of the lophophoral organs can not be held. Individuals without the lophophoral organs build new tubes covered with sand grains just as do those with the organs, and young specimens of *Phoronis architecta*, which are in possession of tubes, never have lophophoral organs. These two facts prove quite conclusively that the lophophoral organs of *Phoronis architecta* are not used for tube building.

Masterman's view that the lophophoral organs of *P. buskii* are glandular, and that they furnish mucus to hold the eggs and embryos in masses can not be applied to *P. architecta*, for in this species the eggs and embryos are not held in masses.

Specimens of *Phoronis architecta* have been examined during almost every month in the year in order to discover whether or not there is any relation between the lophophoral organs and the breeding season During the months of June, July, August, September, and October examination of many specimens of *Phoronis architecta* shows that more than one-half are with lophophoral organs—i. e., with the "carpel-like organs" and the "spherical sense lobes" (Andrews). Examination of specimens taken during these months shows that some contain ovaries and eggs while others do not, and that all contain spermatozoa in the body cavity, but that only those without ovaries contain testes. Occasionally an egg floating freely in the body cavity is found in specimens with testes. These facts are correlated with the presence or the absence of the lophophoral organs, for these organs are present in specimens with testes and without ovaries and absent in specimens with ovaries and without testes.

During the latter part of December and the first part of January specimens of *P. architecta*, some of which were collected in Beaufort Harbor at that time and some of which had been kept alive in the laboratory of Johns Hopkins University since the summer months were examined.

Many of these specimens (30 or 40) were examined by crushing the posterior end and also by cutting sections, but with one exception all of these individuals were found to be without ovaries and testes. In the case of the exception, a few ovarian eggs were present, but the ovaries were still very young. The blood caeca at this time are surrounded by a great abundance of the peculiar peritoneal tissue, which later gives rise to the reproductive organs. Lophophoral organs were absent both in specimens collected at Beaufort during the first part of January and in specimens collected during the summer and kept in the laboratory.

During the months of February, March, and April the specimens in the aquaria at Johns Hopkins University were examined quite frequently, but until March or April there was no sign of lophophoral organs. Then they began gradually to develop in some specimens until by the first of May they were full size. At this time another lot of live material was received from Beaufort which afforded some very interesting observations. The number of individuals with and without lophophoral organs were in about the same ratio as during the summer months. At this time, in specimens with lophophoral organs, the testes are present but the ovaries are not, while specimens without lophophoral organs possess ovaries and contain ovarian eggs. Quite often specimens with lophophoral organs have large bunches of spermatozoa floating freely in the body cavity, and in some cases these occur inside the nephridia. In one individual a large bunch of spermatozoa was found lodged in the end of the lophophoral organ's pocket-like cavity.

Judging from our observations, it seems that the relation of the lophophoral organs to the breeding season is as follows: Some adults are giving rise to eggs throughout the months of May, June, July, August, September, and October. None of the individuals arising from these eggs become sexually mature until March or April of the next year. Those which are the oldest i. e., those born in the early months of the year before—develop testes and lophophoral organs in March or April. Then they lose their lophophoral organs, the testes disap-

pear and ovaries begin to develop about the first of May. While this is going on, individuals which were born later in the summer of the year before begin to develop testes and lophophoral organs, and thus we have individuals with lophophoral organs and testes occurring at the same time of the year as individuals without lophophoral organs and with ovaries.

While there is no absolute proof, the upper part at least of the lophophoral organs probably functions as a kind of seminal receptacle. We are led to this conclusion by these facts: First, that the organs appear only when the testes are present; second, that large bunches of spermatozoa have been found in the body cavity, in the nephridia, and in the cavity of the lophophoral organs; and, third, that there are ciliated grooves leading from the nephridial pores to the cavities of the lophophoral organs.

Vascular system.—Nearly all of the early investigators of the anatomy of *Phoronis* recognize the existence of an efferent and afferent vessel which are in connection with vessels running up into the tentacles.

Caldwell's (3) description, although brief, is complete, and differs very little from later ones. Cori's (4) account seems to be about the same as Caldwell's; however, he recognizes one ring vessel instead of two and describes in more detail the relation between the tentacular vessels and the ring vessel.

In *Phoronis australis*, Benham (2) finds the circulatory system much the same as Caldwell does in the form that he worked on. Practically the only point of difference is that he describes the tentacular vessels as dividing into two branches, one opening into the distributing vessel (inner) and the other into the recipient vessel (outer).

Andrews (1) finds that the vascular system of *P. architecta*, as far as he has determined, is like that of *P. australis*, while Ikeda (9) says that Benham's description holds good for *P. ijimai* and *P. hippocrepia*.

A transverse section through the lophophoral crown of *P. architecta* (fig. 63) shows that the cavity of each tentacle contains a blood vessel which is attached to the inner surface of the wall.

At the base of the tentacles a cross section shows that there are two blood vessels running parallel to one another through most of their course around the cavity of the lophophore (figs. 65 to 71). These vessels are distinct, although closely applied to one another, thus differing from what Cori finds in *P. psammophila*. The outer vessel and inner vessel (figs. 65, 66) are, respectively, the "recipient" and "distributing" vessels which Benham describes. In fig. 83 is shown a cross section through the base of the tentacles. Throughout most of the section the tentacular vessels open into the outer or recipient vessel, but at one end the tentacular vessels open into the inner or distributing vessel. This section, together with sections anterior and posterior to it, show conclusively that the tentacular vessel has two separate openings, one into the distributing vessel, the other into the recipient vessel, and that the distributing and recipient vessels are completely separate. A longitudinal section through the anterior end of *Phoronis architecta* shows conclusively that the tentacular vessel divides into two branches, one opening into the recipient vessel and the other into the distributing vessel.

A little more posteriorly the ring-like distributing vessel opens into a median longitudinal vessel lying between the œsophagus and rectum but close to the wall of the former (figs. 67, 68). This vessel, which is the afferent vessel, pierces the transverse septum (fig. 69) and runs posteriorly (within the rectal or posterior chamber) between the two arms of the alimentary canal. At the point where the vessel passes through the septum there is a thick layer of muscle fibres surrounding the former which undoubtedly has the power of shutting off the blood supply to the tentacles and which may be very necessary to prevent the animal from bleeding to death when the lophophoral crown is cast away (figs. 68 to 71).

The two sides of the ring-like recipient vessel do not pass into a single vessel while they are within the supraseptal cavity (figs. 67 to 71), but after they have pierced the transverse septum the right side of the ring is seen to pass diagonally across the œsophagus and to meet the left side of the ring (figs. 75 to 78). From this point the two become one vessel, the efferent vessel, which runs posteriorly within the left body cavity. In the posterior part of the body, where the alimentary canal makes a loop, the efferent and afferent vessels are continuous and open into

a sinus around the stomach. Along most of the course of the efferent vessel blood caeca are given off, and a large bunch also arises from the sinus.

Nervous system.—We have found that the nervous system of the *Actinotrocha* is more highly developed in some species than in others and that it is subepidermal in character. In the different species of the adult we also find that there is considerable difference in the degree of development of the nervous system and that it is largely subepidermal.

Caldwell (3) was the first to give a good description of the nervous system, although Kowalevsky (11) recognized the existence of a lateral nerve and ganglion. Caldwell found the ring nerve, a hollow nerve cord on the left side, and he speaks of two ciliated pits consisting of nerve cells, ganglion, and nerve fibres. The description is so brief, that one can not say whether or not the ganglion that he speaks of represents the ganglion that Kowalevsky (11) and Cori (4) describe.

Benham (2) finds no ganglion in *P. australis*, but describes two small areas which, it seems probable, are the same as Caldwell's "ciliated pits." He is the first to recognize the existence of a lateral nerve on the right side as well as on the left, and he finds a nerve ring with a nerve to each tentacle arising from it.

Cori (4) describes a definite ganglion, a lateral nerve on the left side only and tentacular nerves. He is the only investigator who has published anything on the distribution of the nervous tissue in the lophophoral organ.

Andrews (1), Torrey (22), and Ikeda (9) have given very brief descriptions of the nervous system, but the two former recognize the existence of a short lateral nerve on the right side as well as a long one on the left side, while the latter speaks of a so-called brain ganglion and nerve ring.

The account which Andrews gives of the nervous system of *P. architecta* is very brief, since his paper deals only with the description of a new species. He only speaks of the lateral nerve and makes no mention of a brain ganglion, ring nerve, tentacular nerves, or nerves to the lophophoral organ.

In general our observations on the lateral nerve of *P. architecta* agree with those of Andrews and Torrey. The lateral nerve of the left side is quite conspicuous and extends from the anterior end to a point about one-third from the posterior end of the animal. It runs along the lateral body wall until it is almost in the region of the transverse septum, then it gradually passes obliquely upward in close proximity to the left nephridial canal, and finally is seen embedded in the ectoderm at the side of the anal papilla. From this point it passes around the base of the anal papilla between the anus and the mouth, and then it begins to take the same course close to the nephridial tube on the right side as it did on the left side, but it soon grows much smaller in diameter and finally disappears (figs. 78 to 67). A longitudinal section passing through the mouth and anus shows the relation which the nerve cord bears to the ganglion and nerve ring (fig. 84). Cori (4) figures such a section through *P. psammophila*, but he seems to have overlooked the nerve cord or axis cylinder in this region. It is closely associated with the cells of the ganglion and lies just a little below the latter. In an oral direction from the ganglion is seen a section through the nerve ring.

If a cross section (fig. 85) is taken through the ganglion so as to cut longitudinally through the nerve cord and if the section is stained deeply with iron haematoxylin and eosin, it will show plainly that there is no cavity in the cord, but that it is made up of a mass of fibres surrounded by a nucleated sheath. Caldwell (3) considers the structure to be a hollow nerve cord; Benham (2) says that it has semifluid contents and that he has been unable to make out any punctated nerve substance; and Cori (4) states that it is an axis cylinder.

We have endeavored to find some connection between the cord and the ganglion, but have not been very successful. In the region of the ganglion—i. e., between the mouth and the anus—the sheath of the nerve cord does not seem to differ in thickness or character from the same structure in other parts. The cells of the ganglion, however, send out processes which in sections are frequently seen applied to the sheath, but no connection between the fibres of the nerve ring and those of the cord could be made out.

Kowalevsky (11), Cori (4), and Torrey (22) have all found the nerve ganglion, while Benham (2) denies its existence in *P. australis*. It undoubtedly exists in *P. architecta*, is situated at the base of the anal papilla between the anus and the mouth, and lies above the nerve cord between the anal papilla and the nerve ring (fig. 84).

The ganglion consists of nerve fibres and nerve cells and the latter have at least two processes. While it is a definite structure back of the anal papilla, on the sides it diminishes in size until its cells become indistinguishable from those of the nerve ring. In fact, all of the ectoderm forming the sides of the groove between the anal papilla and the base of the lophophore is rich in nerve fibres and cells.

The nerve ring follows the base of the lophophore on the outer side throughout its extent, and in the inner part of the horseshoe it is quite rich in nerve cells whose processes can be seen penetrating into the mass of fibres (figs. 67 to 74). This ring represents the collar nerve ring of the *Actinotrocha*.

There is a definite tract of nervous tissue running up the inner side of the tentacle, but we are not prepared to say that it is a nerve running from the ring, although it is nervous tissue which is undoubtedly continuous with that of the nerve ring.

Cori (4) has carefully studied the anatomy of the lophophoral organ of *P. psammophila* and we have nothing to add to his description at present. We are also unprepared to say whether or not the second layer of the lophophoral organ consists of nerve cells. As he has described, they have long prolongations which extend from the cells of the inner layer to the outer, and these processes form a rather marked layer just below the epidermis on the outer surface of the organ. At the base of the lophophoral organ these prolongations seem to be intimately associated with nerve fibres which can be traced to the nerve ring.

Throughout the body wall of the trunk there is a subepidermal layer of nervous tissue.

Nephridia.—We have nothing new to add concerning the adult nephridia, but our observations on *P. architecta* confirm those of Benham (2) for *P. australis*. The nephridial canals lie embedded in the ectodermal wall in the region of the rectum. Each opens to the exterior through a pore at the side of the anal papilla. Following the canal from the nephridial pore, we see that it passes downward—i. e., posteriorly—for a short distance and then bends upon itself running upward parallel to the descending arm. A short distance above the bend it opens by one funnel into the lateral body cavity (fig. 72) and by another into the rectal body cavity (fig. 70).

Reproductive organs.—Ikeda's recent paper (10) on the reproductive organs of *Phoronis* gives a good account of the anatomy and development so we shall not enter into a description of them. We are able to confirm Andrews's observations that the male organs develop at a different time from those of the female.

Ciliated ridge of the alimentary canal.—Andrews has described a ridge running along the inner wall of the oral branch of the alimentary canal (fig. 81). H. B. Torrey has found the same structure in *P. pacifica*, and we can confirm Andrews's observation for *P. architecta*. This ridge does not seem to have any rudiment in the *Actinotrocha*, and it is not present just after metamorphosis.

SUMMARY.

The male and female reproductive organs do not develop at the same time in *P. architecta*, and the indications are that it is a protandrous animal.

Fertilization is external and the eggs are not held in lophophoral masses by the tentacles.

Segmentation is holoblastic and equal, but cleavage does not occur simultaneously in all the blastomeres. During the division of the four-cell stage into the eight-cell stage, the upper four blastomeres rotate in the direction of the hands of a watch. The sixteen-cell stage arises from the eight-cell stage by a meridional division of each blastomere.

The blastopore is eccentric from the beginning of gastrulation and the ganglion of the *Actinotrocha* makes its appearance at this time. As development proceeds, the blastopore gradually closes up from the posterior end toward the anterior end of the larva until finally it becomes a transverse slit.

The "primitive streak" of Caldwell does not seem to be present in the larva of *P. architecta*.

The "nephridial pit" is of ectodermal origin.

The mesoderm arises, for the most part, from the lips of the blastopore. Archenteric diverticula are not present in the larva of *P. architecta*, but there is a sac-like formation of mesoderm cells in the anterior end which forms the lining of the preoral lobe and which gives rise to a mesentery between the lobe and collar cavities.

The lining of the collar cavity does not arise from a mesodermal sac. It is formed by isolated mesoderm cells which arrange themselves on the somatic wall leaving the splanchnic wall practically without any lining.

In the larva of *P. architecta* the mesodermal lining of the trunk cavity is complete, covering both the somatic and splanchnic walls, and it seems probable that it arises from cells forming the base of the nephridial diverticula. There is a mesentery between the cavities of the trunk and collar.

A stomodæum and proctodæum are not present. The blastopore becomes the mouth, the anus arises quite late in the early life of the embryo, and the rectum is formed as an outgrowth of the blind end of the archenteron.

The nephridial canals, at least, have their origin in a single median pit which soon branches into two intercellular tubes. We have not found any evidence that the excretory cells of the nephridia are formed from free mesoderm cells attaching themselves to the blind end of the nephridial canals.

The "neuropore" and "subneural gland," which Masterman has described, do not exist in the *Actinotrocha* examined, although imperfectly preserved specimens show unusual structures which might be taken for these organs.

Masterman's "subneural sinus" is not present either, although there is a space below the ganglion which is free from mesodermal strands. The "atrial grooves" which Masterman says exist are present in the larvæ we have studied, but we can not consider that they have the significance that he assigns to them. Occasionally grooves are found which might be comparable to Masterman's "oral grooves," but they are due to imperfect fixation. The stomach diverticula exist in one species that we have examined, but they do not impress us as being of notochordal nature, as Roule and Masterman have claimed.

There is a subepidermal layer of nervous tissue throughout the body. Extending anteriorly from the ganglion, which is situated on the median dorsal surface of the hood, are three longitudinal nerves, which finally become continuous with a nervous ring running around the edge of the hood. From the posterior side of the ganglion two parallel tracts of nerve fibres issue and pass posteriorly along the dorsal collar wall until they reach the circle of tentacles, where most of them follow the line of insertion of the collar trunk mesentery, and give rise to a collar nerve ring. The nerve fibres from the edge of the preoral hood do not pass up to the ganglion from the point of attachment of the hood on to the collar wall, as Masterman has described, but they make a sharp turn, running posteriorly and obliquely along the lateral and ventral wall of the collar, where they form two definite nerve tracts which become lost in the region of the collar nerve ring. While there may be nerve fibres passing from the ganglion out in all directions over the surface of the hood, we have not been able to make them out, nor do we find any definite nervous tract running along the dorsal or ventral wall of the trunk segment.

There is one pair of retractor muscles extending from the region of the ganglion to the collar walls, in the region of the first and second pairs of tentacles, and besides these, in one *Actinotrocha* that we have examined, there is another pair extending from the sides of the ganglion to the ventral wall of the hood. In this latter *Actinotrocha* there is an extensive layer of muscle fibres in the wall of the hood and also a ring of fibres around the edge of the latter. A pair of longitudinal muscle tracts extend from the region of the ganglion, along the dorsal wall of the *Actinotrocha*, to the perianal ring, and there is a similar pair of tracts extending along the ventral wall of the collar and trunk. A ring of muscle fibres run parallel with the ring nerve, between the collar and trunk segments. Beside these muscle tracts there is a layer of circular fibres in

the wall of the collar and trunk, lying between the longitudinal fibres and the ectoderm. There is also a covering of muscle cells on the ventral pouch and on the wall of the dorsal blood vessel.

The nephridia have much the same structure as those of *Amphioxus*, as described by Goodrich. In one of the *Actinotrochæ* from Beaufort Harbor the nephridial canal branches, but in the other it does not. Nephridial funnels do not exist, but the ends of the canals open into tubular cells, and the lumen of each cell contains a flagellum. The nephridial canals open to the exterior, at the sides of the orifice of the ventral pouch. The nephridia, which Masterman describes for the preoral hood and trunk, are not present in any *Actinotrochæ* that we have examined.

The blood vessels of the *Actinotrocha* are formed from the splanchnic mesodermal lining and they inclose part of the blastocœle. There is a dorsal blood vessel opening (?) anteriorly into the space between the stomach wall and the splanchnic lining. At the posterior end of the stomach, where the dorsal vessel ends, there are cæcal vessels formed as evaginations of the mesodermal lining of the stomach. The dorsal vessel becomes the afferent vessel of the adult, while the efferent vessel does not arise until just after metamorphosis. The collar cavity, which is a part of the blastocœle, becomes the ring vessels and tentacular vessels of the adult. There is no connection between the dorsal blood vessel and Masterman's "subneural sinus."

The blood corpuscles arise from the somatic mesodermal lining of the ventro-lateral collar wall just in front of the septum. They make their appearance as two masses of cells bilaterally placed, one on each side of the median ventral line, and as they develop they migrate across the collar cavity and become applied to the naked walls of the stomach.

The rudiment of the supraseptal or collar cavity of the adult makes its appearance in about the same region as do the blood corpuscles but a little later in the life history of the *Actinotrocha*.

During metamorphosis the following organs are lost: The preoral lobe, the ganglion, and the larval tentacles. The ectodermal wall of the collar cavity, the stomach diverticula, the digestive areas, and the perianal ciliated ring are not destroyed, but they lose their identity. The subepidermal nervous layer of the trunk and ventral pouch becomes part of the same tissue in the adult, but the larger part of this tissue, as well as the lateral nerve, the ganglion, and the nerves to the lophophoral organs are new formations.

All of the nervous structures of the collar and trunk are lost during metamorphosis, except the collar trunk nerve ring, which persists as the nerve ring of the adult.

The ventral mesentery becomes the œsophageal and rectal mesenteries of the adult, and the cavities of the trunk and ventral pouch are transformed into the infraseptal cavity.

At least the greater part of the nephridia is lost during metamorphosis.

The lophophoral organs arise late in the adult life and are present only in individuals which are with testes and without ovaries. They probably serve as seminal receptacles.

The vascular system of the adult consists of an efferent and afferent vessel, which are continuous posteriorly by means of a sinus around the loop of the alimentary canal; of cæcal vessels as outgrowths from the afferent vessel and the blood sinus; of a distributing and recipient ring vessel, the former opening into the afferent vessel and the latter into the efferent vessel; and of tentacular vessels, each of which divides into two short branches, one opening into the distributing vessel and the other into the recipient vessel.

There is a ciliated ridge extending along part of the inner wall of the alimentary canal.

The nervous system of the adult is to a great extent subepidermal. There is a nerve with a nucleated sheath extending along the left side of the animal. Anteriorly it bends around the anal papilla and continues as a short nerve on the right side. There is a ganglion between the mouth and anus. A nerve ring extends around the base of the lophophore and it gives off nerves to the lophophoral organs. There is nervous tissue in the walls of the tentacles.

The excretory organs are paired and each nephridium consists of a tube bent upon itself. One end opens to the exterior, while the other is continued into two funnels, one communicating with the rectal and the other with the lateral body cavity.

The reproductive organs arise from the lining of the cæcal blood vessels, and the male organs develop at a different time from those of the female.

JOHNS HOPKINS UNIVERSITY, *March, 1904*.

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[a] Received after completion of paper.

REFERENCE LETTERS FOR FIGURES.

a .... anus.
a. c. c .... adult collar cavity (Ikeda).
af. v .... afferent blood vessel.
al. c .... alimentary canal.
a. p .... anal papilla.
art .... artefact.
a. t .... adult tentacle.
a. t. m .... transverse septum of adult.
b. c .... blood corpuscles.
b. c. m .... blood corpuscle masses.
b. t .... basement tissue (Benham).
cæ .... blood cæcum.
c. c .... collar cavity.
c. g .... ciliated groove (Andrews).
c. w .... collar wall.
d. a .... digestive area.
d. m. t .... dorsal muscle tract.
d. v .... dorsal vessel (afferent).
d. ve .... distributing vessel.
ef. v .... efferent vessel.
eg .... egg.
e. h .... edge of hood.
ep .... epistome.
ex. c .... excretory cell.
fl .... flagellum.
g .... ganglion.
g. c .... ganglion cell.
g. m. c .... giant mesoderm cell.
in. c .... infraseptal cavity.
int .... intestine.
lat. n .... lateral nerve.
l. l. c .... left lateral cavity.
l. l. m .... left lateral mesentery.
l. l. n .... lateral longitudinal nerve.
l. m .... longitudinal muscle.
l. r. m .... ring muscle tract of lobe.
l. r. n .... ring nerve tract of lobe.
l. t .... larval tentacle.
m .... mesoderm.
m.[1] .... mesentery between preoral lobe and collar cavities.
m.[2] .... mesentery between collar and trunk cavities.
m. c. m .... mesodermal cell mass giving rise to blood corpuscles.
m. f .... muscle fiber.
m. l. n .... median longitudinal nerve.
m. s .... mesodermal sac of preoral lobe.
n. c .... nephridial canal.
neph .... nephridium.
neph. o .... nephridial opening.
n. f .... nerve fiber.
n. f.[1] .... nephridial funnel into rectal body cavity.
n. f.[2] .... nephridial funnel into lateral body cavity.
n. p .... nephridial pit.
nu .... nuclei of ciliated cells of perianal ring.
œs. m .... œsophageal mesentery.
p. an. s .... perianal space.
pig .... pigment.
p. o. c .... preoral body cavity.
p. o. l .... preoral lobe.
p. r .... perianal ring.
p. re .... posterior recess (Ikeda). subneural sinus (Masterman).
r .... rectum.
r. b. v .... ring blood vessel.
r. c .... rectal cavity.
r. d. m .... rudimentary dorsal mesentery.
ret .... retractor muscle.
r. l. c .... right lateral cavity.
r. m .... rectal mesentery.
r. n .... ring nerve.
r. ve .... recipient vessel.
sen. p .... sensory papilla.
sp. m .... sphincter muscle.
st .... stomach.
sup. c .... supraseptal cavity.
t .... tentacle.
t. b. v .... tentacular blood vessel.
t. c .... trunk cavity.
th .... ventral thickening of ectoderm.
t. m. t .... tentacular ring muscle tract.
t. n. t .... tentacular ring nerve tract.
t. r .... tentacular ridge.
v .... vestibule.
ves .... glandular vesicles in ectoderm.
v. m .... ventral mesentery.
v. m. t .... ventral muscle tract.
v. n. t .... ventral nerve tract.
v. p .... ventral pouch.
v. p. o .... ventral pouch opening.
v. v .... ventral blood vessel (efferent).
v. w. h .... ventral wall of hood.

EXPLANATION OF FIGURES.

The objectives used in this work are the ⅔ and ⅙ Spencer and the 1/12 Zeiss Oil Immersion. The oculares used are the " - 4" and " - 8" Spencer and the No. 12 Zeiss Compensating.

PLATE I.

PLATE I.

Fig. 1.—Transverse section through nephridium of adult. $\frac{1}{12}$ Ob. × 4 Oc. Camera. × 440.

Fig. 2.—Unsegmented egg with one polar body. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 3.—Two-cell stage, showing equal blastomeres. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 4.—Two-cell stage, showing unequal blastomeres. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 5.—Beginning of two-cell stage. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 6.—Section through two-cell stage. Chromosomes have lost their identity and granular vesicles have made their appearance. Granular character of the yolk only shown in part of one blastomere. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 7.—Beginning of four-cell stage. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 8.—Four-cell stage, showing polar furrow. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 8*a*.—Section through four-cell stage, showing granular vesicles which make their appearance after the disappearance of the chromosomes. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

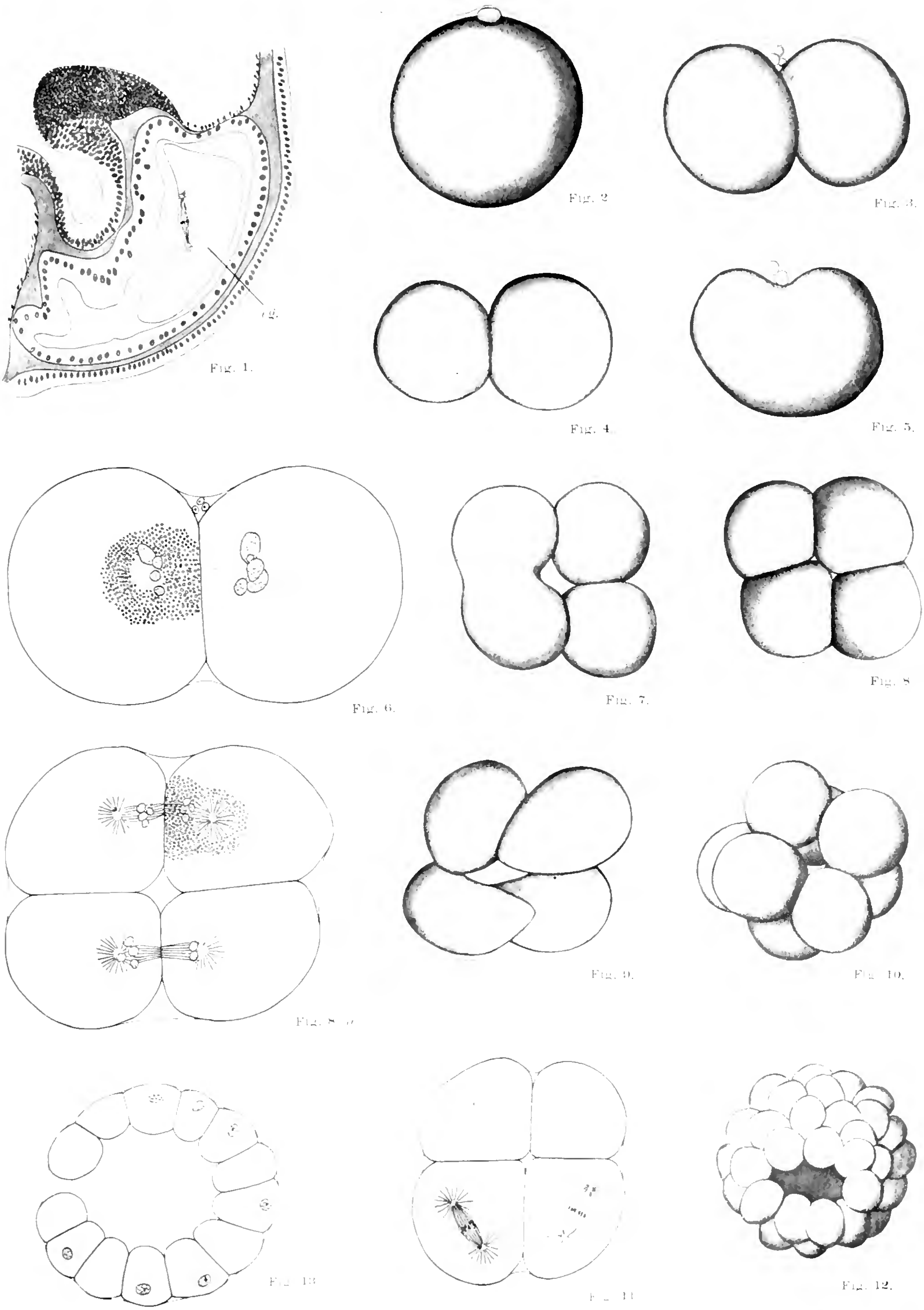
Fig. 9.—Four-cell stage passing into eighth-cell stage. Seen from above and showing the twisting of the blastomeres. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 10.—Eight-cell stage, showing rotation of blastomeres. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 11.—Section of eight-cell stage ready for sixteen-cell stage. Position of mitotic figures indicate meridional division. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 12.—Young blastula showing "blastocœle pore." (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 13.—Section through young blastula showing blastocœle pore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.



PHORONIS ARCHITECTA

PLATE II.

PLATE II.

Fig. 14.—Optical section of an old blastula. (From life.) $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 360.

Fig. 14*a*.—Section through an old blastula showing endodermal bodies in blastocœle. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 15.—Longitudinal section through older blastula than that of fig. 14*a* showing proliferation of endoderm cells. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 15*a*.—Transverse section through a gastrula which is just beginning to gastrulate. Taken through ganglionic thickening. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 15*b*.—Transverse section through same specimen as that of fig. 15*a*. Taken through the middle of the gastrula. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16.—Longitudinal section through a gastrula which has begun to elongate. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*a*.—Transverse section through anterior end of a gastrula which was a little younger than that of fig. 16. Taken just back of the ganglion. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*b*.—Transverse section through same specimen as that of fig. 16*a*. Taken just in front of anterior end of the archenteron. Shows mesoderm arising from the latter. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*c*.—Continuation of above series. Taken through anterior part of archenteron. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*d*.—Continuation of above series. Taken through middle of archenteron. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*e*.—Continuation of above series. Taken through posterior part of archenteron. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*f*.—Continuation of above series. Taken through the region where the lips of the blastopore are closing up. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 16*g*.—Horizontal section through a gastrula of the same age as that of fig. 16. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

Fig. 17.—Transverse section through a gastrula showing peculiar granular cells arising from the endoderm. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

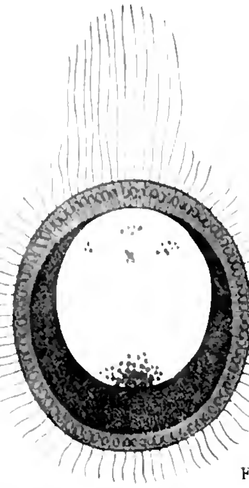


Fig. 14.

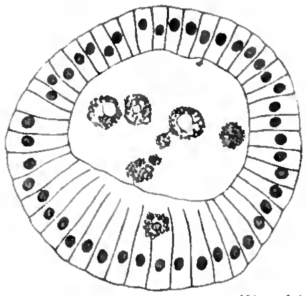


Fig. 14 (a)

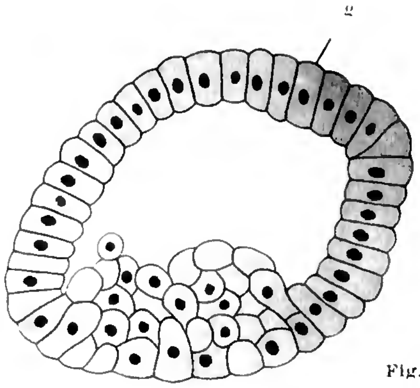


Fig. 15.

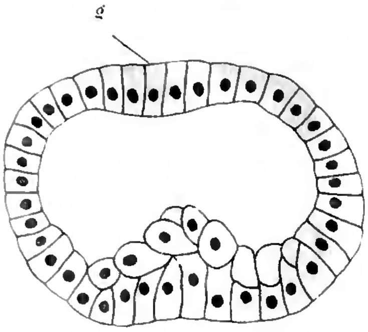


Fig. 15 (a)

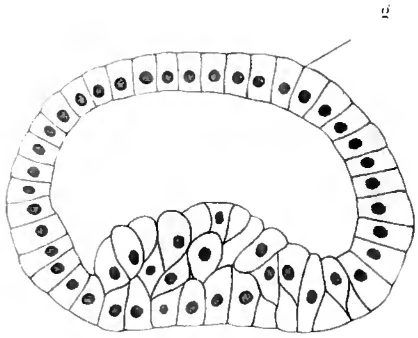


Fig. 15 (b)

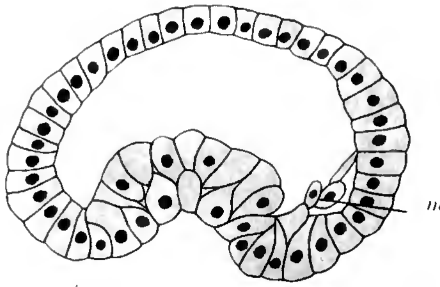


Fig. 16.

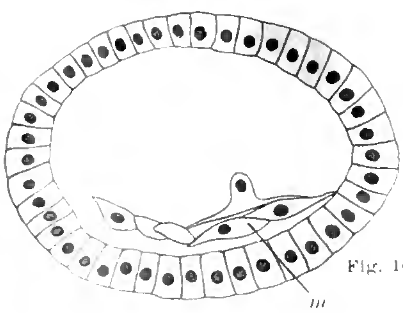


Fig. 16 (a)

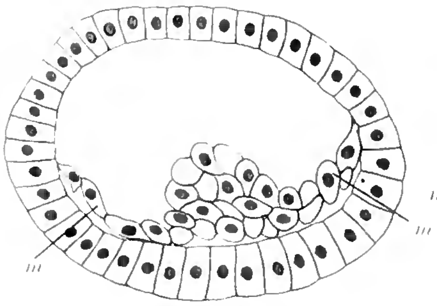


Fig. 16 (b)

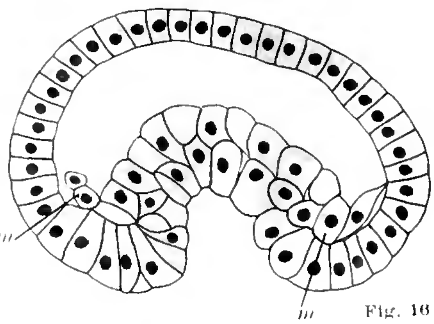


Fig. 16 (c)

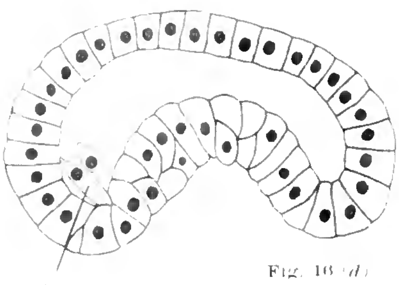


Fig. 16 (d)

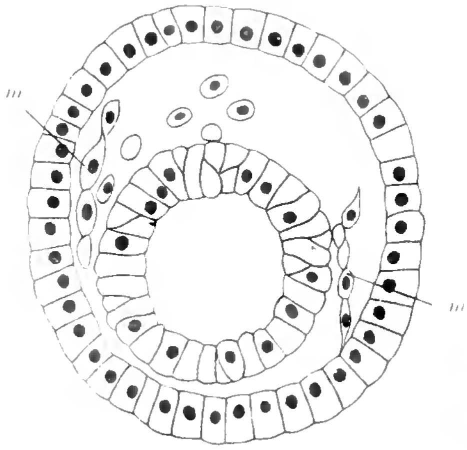


Fig. 16 (g)

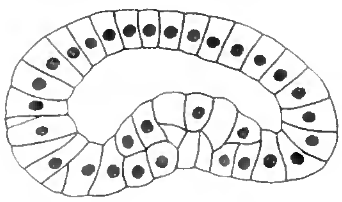


Fig. 16 (f)

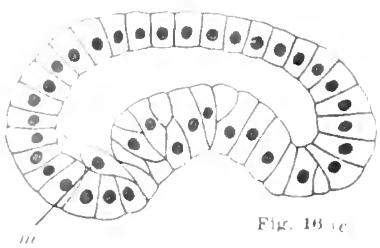


Fig. 16 (e)

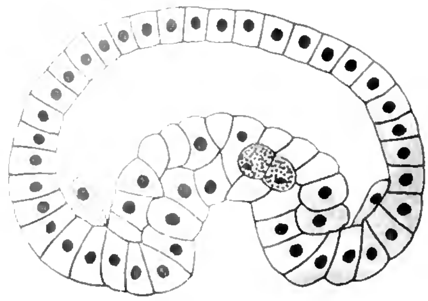


Fig. 17.

PHORONIS ARCHITECTA

PLATE III.

PLATE III.

FIG. 17*a*.—Same as fig. 17, showing one of the peculiar cells set free in the blastocœle. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18.—Transverse section through the anterior end of a young larva, which is slightly younger than the specimen of which fig. 19 is a longitudinal section. Blastopore is slightly oval in outline. Taken through the ganglion. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18*a*.—Continuation of above series. Taken just in front of archenteron. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18*b*.—Continuation of above series. Taken through anterior part of blastopore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704

FIG. 18*c*.—Continuation of above series. Taken through posterior part of blastopore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18*d*.—Continuation of above series. Taken immediately posterior to the blastopore. Lips have grown together and there is a straight furrow corresponding to Caldwell's "primitive groove." $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18*e*.—Continuation of above series. Taken posteriorly to section 18*d*. No sign of Caldwell's "primitive groove or streak." $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 18*f*.—Horizontal section through same stage as 18 *a*, *b*, *c*, etc. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 19.—Sagittal section through larva which is a little older than that of series 18 *a*, *b*, *c*, etc. Shows mesodermal preoral sac. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20.—Sagittal section through a larva somewhat older than that of fig. 19. Blastopore has become circular again, but much smaller than originally. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20*a*.—Transverse section through larva of same age as that of fig. 20. Taken just posterior to the ganglion. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20*b*.—Continuation of series. Taken through blastopore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20*c*.—Continuation of series. Taken just posterior to the blastopore. Slight indication of groove. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20*d*.—Continuation of series. Taken near posterior end of larva. No groove. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 20*e*.—Horizontal section through a larva of the same age as that of figs. 20 *a*, *b*, etc. Shows mesodermal sac with posterior prolongations. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

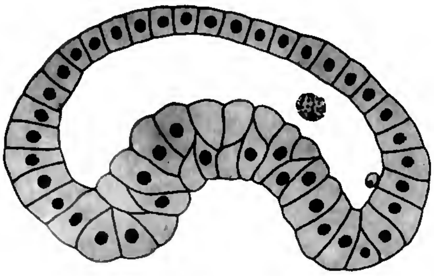


Fig. 17 (*a*)

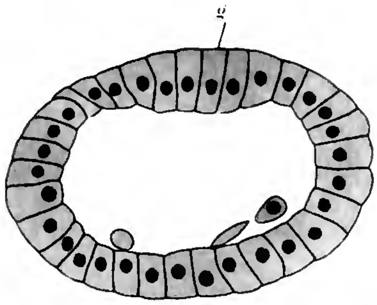


Fig. 18.

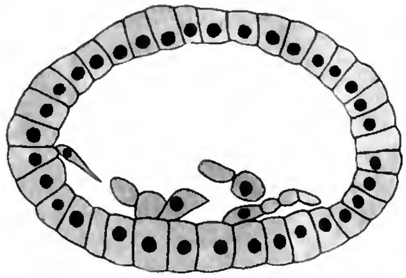


Fig. 18 (*a*)

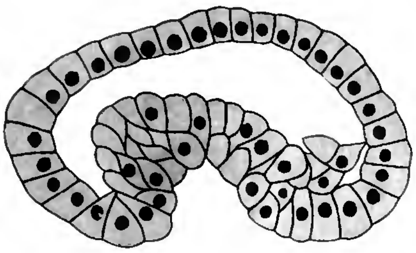


Fig. 18 (*b*)

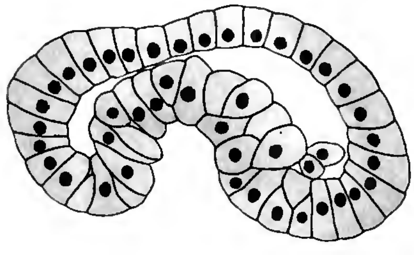


Fig. 18 (*c*)

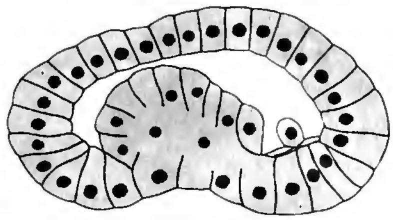


Fig. 18 (*d*)

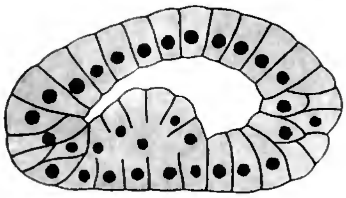


Fig. 18 (*e*)

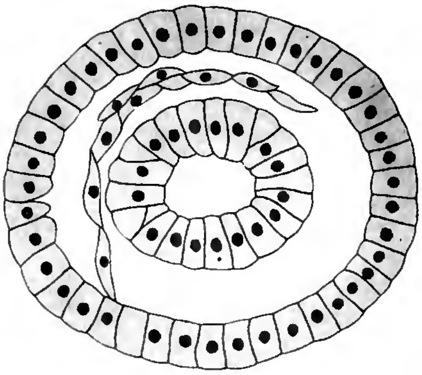


Fig. 18 (*f*)

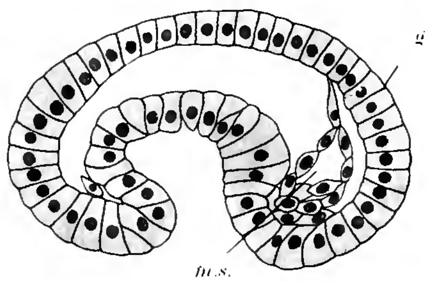


Fig. 19.

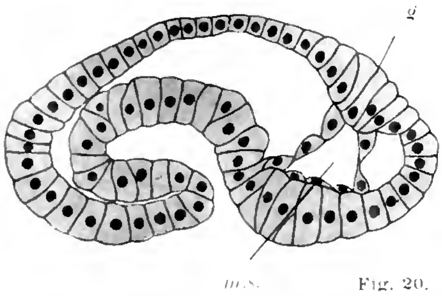


Fig. 20.

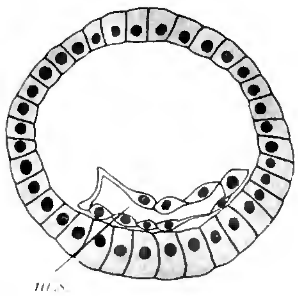


Fig. 20 (*a*)

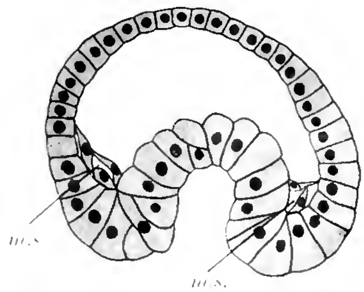


Fig. 20 (*b*)

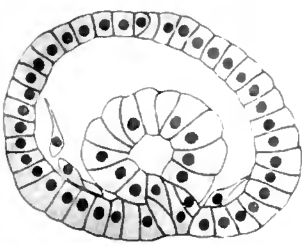


Fig. 20 (*c*)

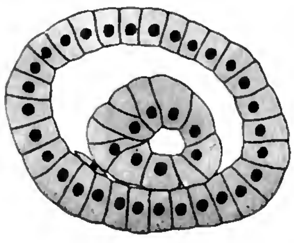


Fig. 20 (*d*)

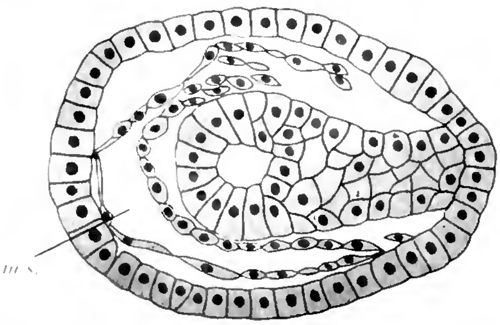


Fig. 20 (*e*)

PHORONIS ARCHITECTA

PLATE IV.

PLATE IV.

FIG. 21.—Sagittal section through a larva somewhat older than that of fig. 20 *a*, *b*, *c*, etc. Blastopore oval and transverse. Nephridial pit present at this stage. Archenteron has fused with posterior ectodermal wall. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 21*a*.—Continuation of above. Taken longitudinally and lateral to that of fig. 21. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22.—Transverse section through a larva of the same age as the one shown in figs. 21 and 21*a*. Taken just posterior to ganglion. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*a*.—Continuation of above series. Taken through blastopore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*b*.—Continuation of above series. Taken just posterior to blastopore. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*c*.—Continuation of above series. Taken halfway between the blastopore and the posterior end. Shows the mesoderm cells on the ventral ectoderm. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*d*.—Continuation of above series. Taken through rectum. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*e*.—Continuation of above series. Next section posterior to that of fig. 22*d*. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*f*.—Continuation of above series. Next section posterior to that of fig. 22*e*. Through wall of nephridial pit. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 22*g*.—Continuation of above series. Section through nephridial pit. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 23.—Horizontal section through a larva of the same age as that of fig. 21. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 23*a*.—Same as fig. 23, but more ventral. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 24.—Longitudinal section through a larva somewhat older than that of fig. 21. Not quite sagittal. Anus has just made its appearance. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 25.—Larva with two pairs of tentacles. (From life.) $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 225.

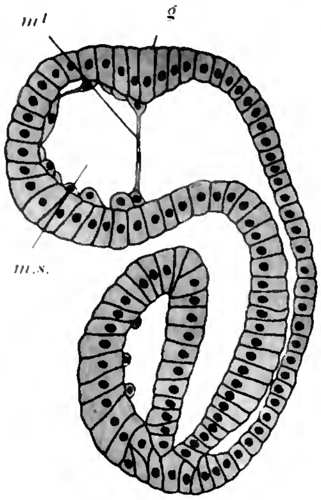


Fig. 21.

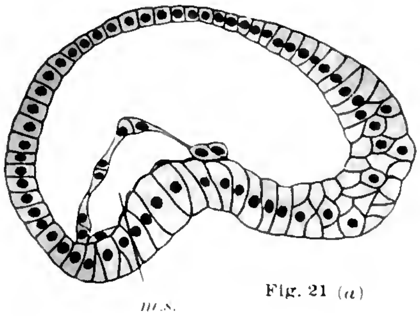


Fig. 21 (a)

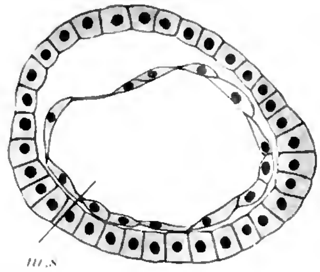


Fig. 22.

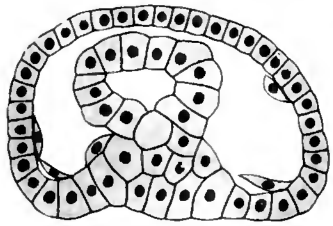


Fig. 22 (b)

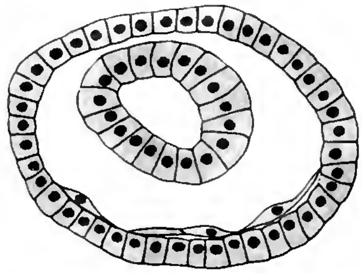


Fig. 22 (c)

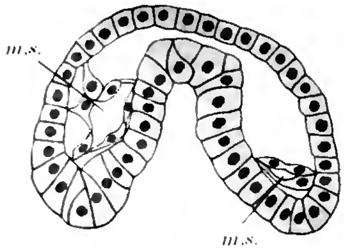


Fig. 22 (a)

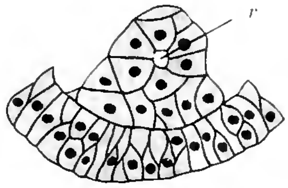


Fig. 22 (e)

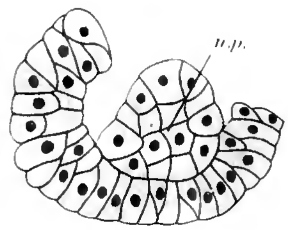


Fig. 22 (f)

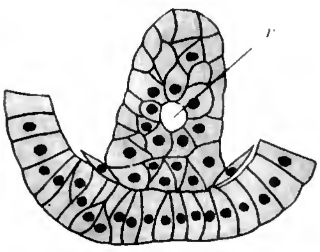


Fig. 22 (d)

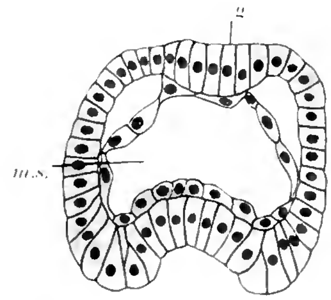


Fig. 23.

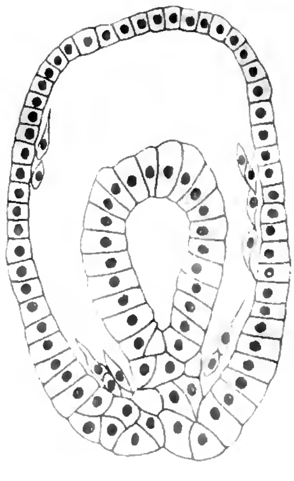


Fig. 23 (a)

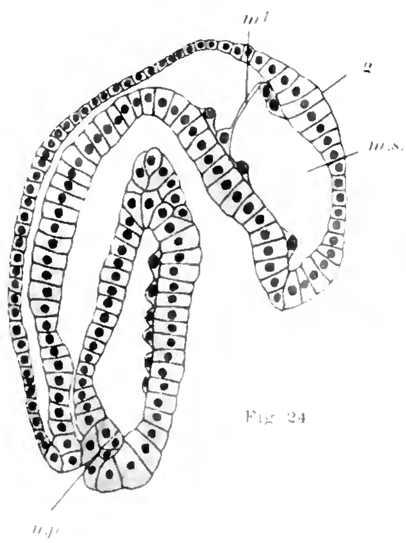


Fig. 24

Fig. 25

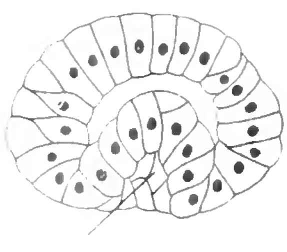


Fig. 22 (g)

PLATE V.

PLATE V.

FIG. 26.—Horizontal section through a larva somewhat older than that of fig. 24, but younger than that of fig. 25. Shows the separation of the cells of the nephridial pit into two wings. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 27.—Horizontal section of posterior end showing slightly older stage in the development of the nephridia than that of fig. 26. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 28.—Horizontal section through a larva with beginnings of two tentacles. Shows nephridia. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 29*a*.—Transverse section through posterior end of a larva with two pairs of tentacles. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 29*b*.—Continuation of series 29*a*. Taken through the region of the rectum. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 29*c*.—Continuation of series 29*a*. Taken through the middle of the larva. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 29*d*.—Continuation of series 29*a*. Taken through the body proper and the lower part of the hood. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 29*e*.—Continuation of series 29*a*. Taken through body and hood near the region of the mouth. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 30.—Almost a sagittal section through a larva with two tentacles. $\frac{1}{12}$ Oil Immersion. × 8 Oc. Camera. × 704.

FIG. 31.—Larva with three pairs of tentacles. Outline drawing from life. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 225.

FIG. 32.—Larva with five pairs of tentacles. Outline drawing from life. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 202.

FIG. 33.—Larva with six pairs of tentacles. Outline drawing from life. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 202.

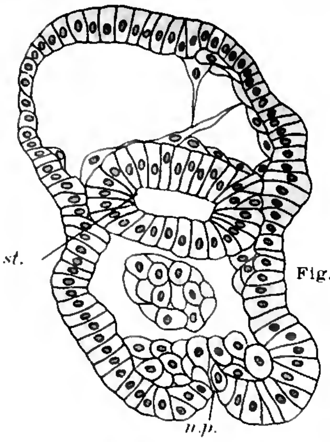


Fig. 26.

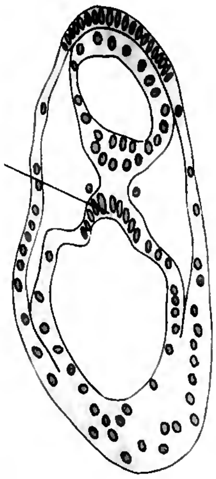


Fig. 29 (d)

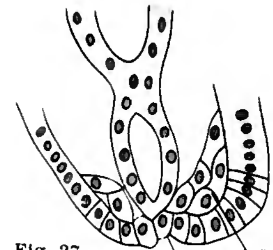


Fig. 27.

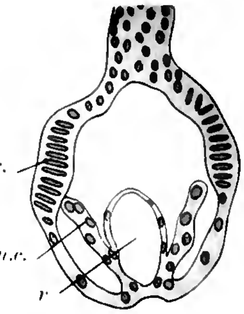


Fig. 28.

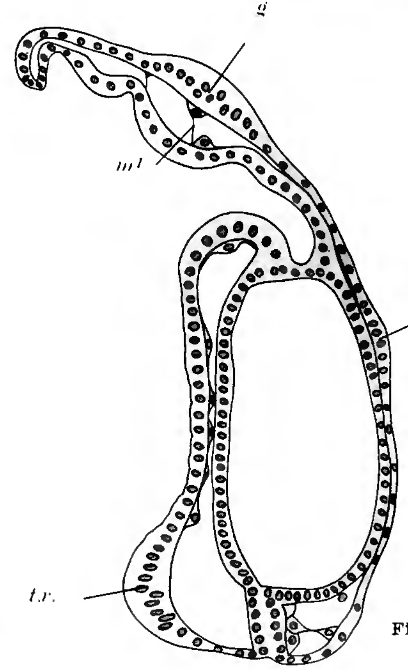


Fig. 30.

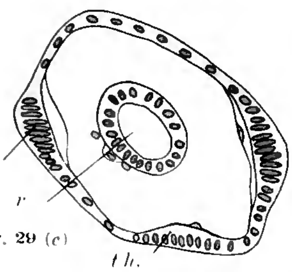


Fig. 29 (c)

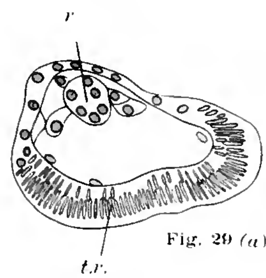


Fig. 29 (a)

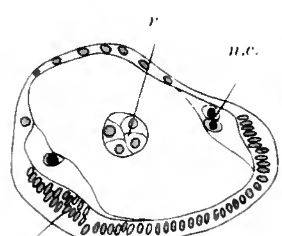


Fig. 29 (b)

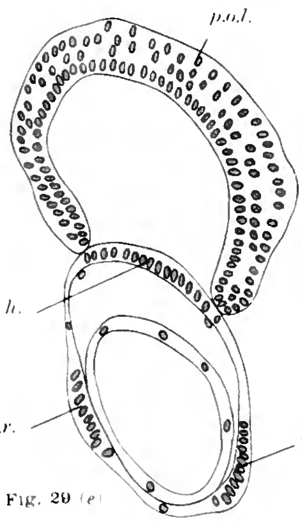


Fig. 29 (e)

Fig. 32.

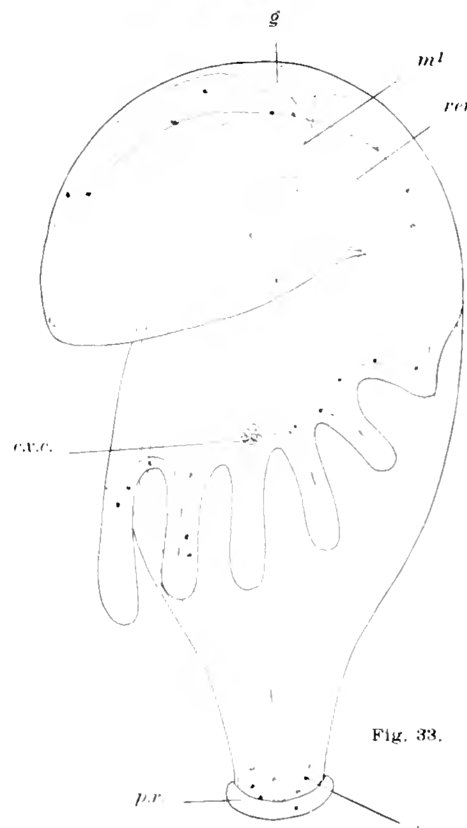


Fig. 33.

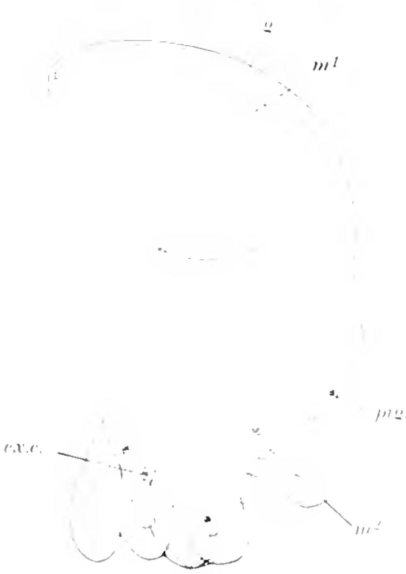


Fig. 31.

PHORONIS ARCHITECTA

PLATE VI.

PLATE VI.

FIG. 34.—*Actinotrocha* Species A. (Drawn from life.) $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 135.
FIG. 35.—*Actinotrocha* Species B. (Drawn from life.) $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 135.

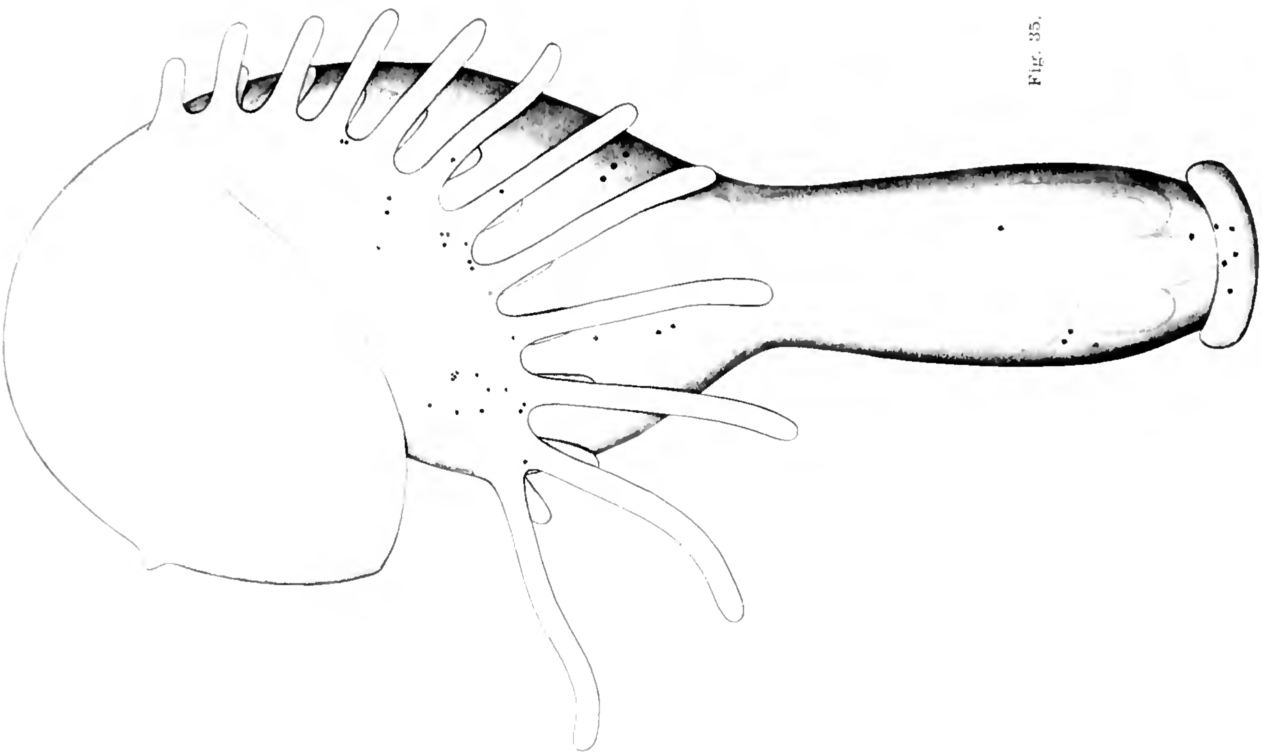


Fig. 35.

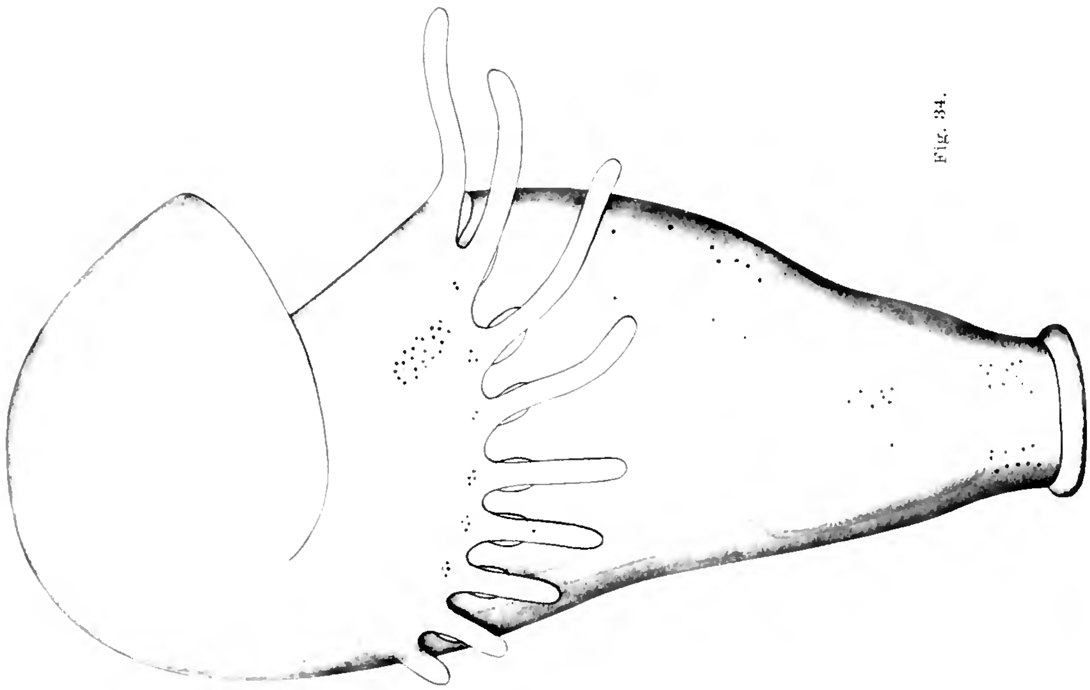


Fig. 34.

PHORONIS ARCHITECTA

PLATE VII.

PLATE VII.

FIG. 36.—Nervous and muscular tracts of the dorsal surface of the hood. *Actinotrocha* Species B. (Drawn from living specimen.)

FIG. 37.—Lateral view of anterior part of *Actinotrocha* Species B., showing muscle tracts. (Drawn from living specimen.)

FIG. 38.—Longitudinal section through the ganglion of an *Actinotrocha*. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Occulare. Camera. × 665.

FIG. 39.—Section through a ganglion cell in the collar nerve ring. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. × 81 Oc. Camera. × 469.

FIG. 40.—Transverse section through the nerve tract of the ventral collar wall. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Occulare. Camera. × 665.

FIG. 41.—Transverse section through the dorsal nerve tract where it passes down along the bases of the tentacles. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Occulare. Camera. × 665.

FIG. 42.—Transverse section through the collar nerve ring. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Occulare. Camera. × 665.

FIG. 43.—Transverse section through the nerve tract around the edge of the hood. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Occulare. Camera. × 665.

FIG. 44.—Transverse section through the hood of *Actinotrocha* Species B. Taken through the sensory papilla. Hood flattened out. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*a*.—Continuation of series 44. Taken through the anterior part of the ganglion. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*b*.—Continuation of series 44. Taken through the ganglion which is invaginated by the action of fixing agents. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

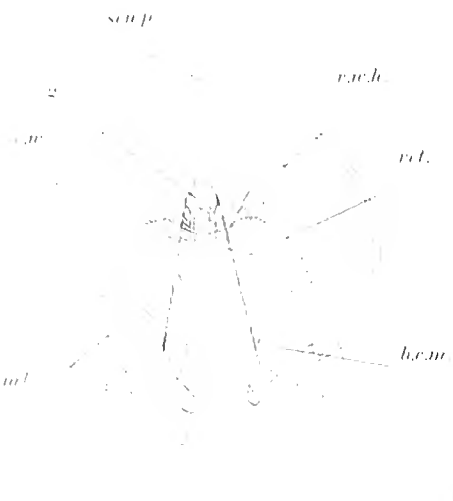


Fig. 36.

Fig. 37.

Fig. 42.

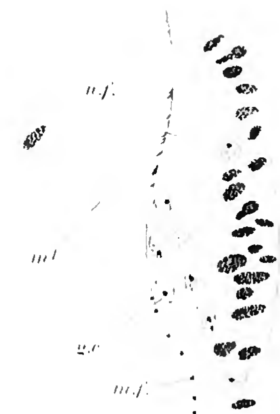


Fig. 38.

Fig. 40.

Fig. 41.

Fig. 39.

Fig. 43.

Fig. 44.

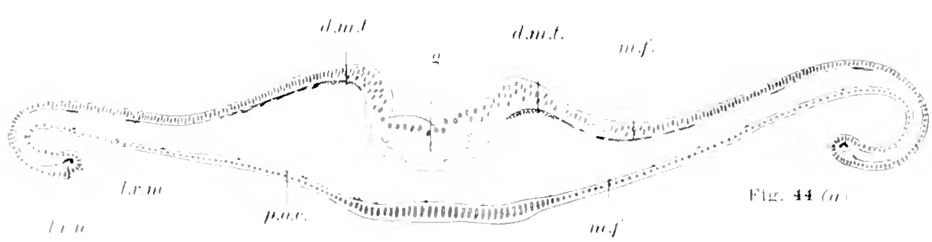


Fig. 44 (a).

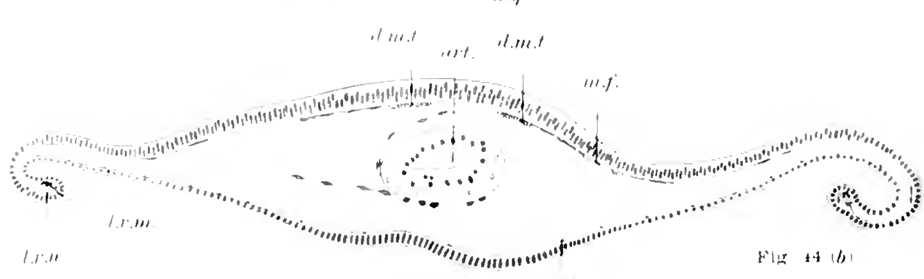


Fig. 44 (b).

PHORONIS ARCHITECTA

PLATE VIII.

PLATE VIII.

FIG. 44*c*.—Continuation of series 44. Taken through the region where the edge of the hood passes into the collar wall. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*d*.—Continuation of series 44. Taken through the middle of the collar segment. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*e*.—Continuation of series 44. Taken through the bases of the ventral tentacles of the collar. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*f*.—Continuation of series 44. Taken immediately posterior to that of fig. 44*e*. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 300.

FIG. 44*g*.—Continuation of series 44. Taken in the anterior part of the trunk segment. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 480.

FIG. 44*h*.—Continuation of series 44. Taken through the rectum. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 480.

FIG. 44*i*.—Continuation of series 44. Taken through the anterior part of the perianal ring. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 480.

FIG. 44*j*.—Continuation of series 44. Taken through the posterior part of the perianal ring. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 480.

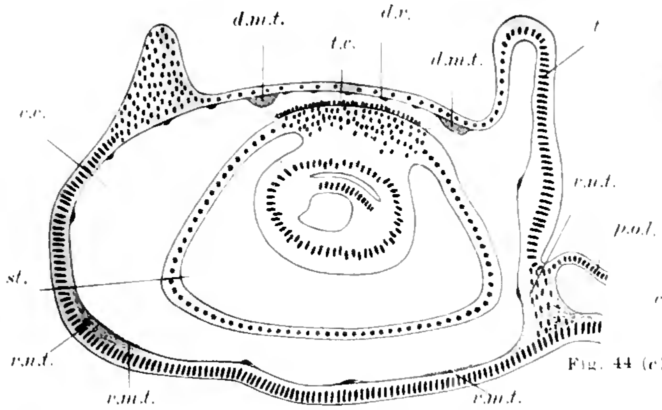


Fig. 44 (c)

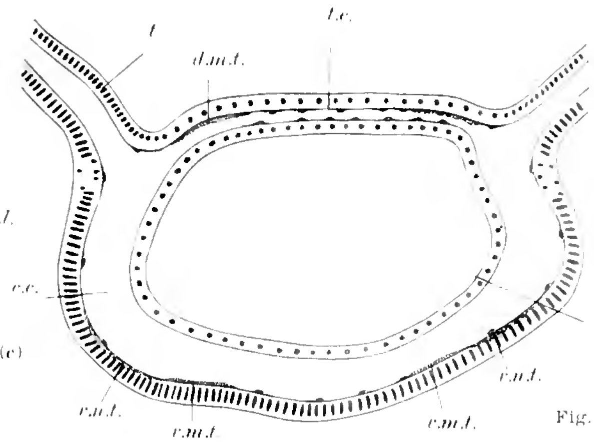


Fig. 44 (d)

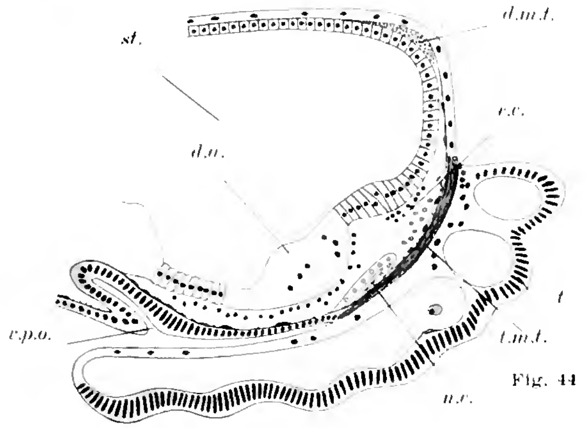


Fig. 44 (e)

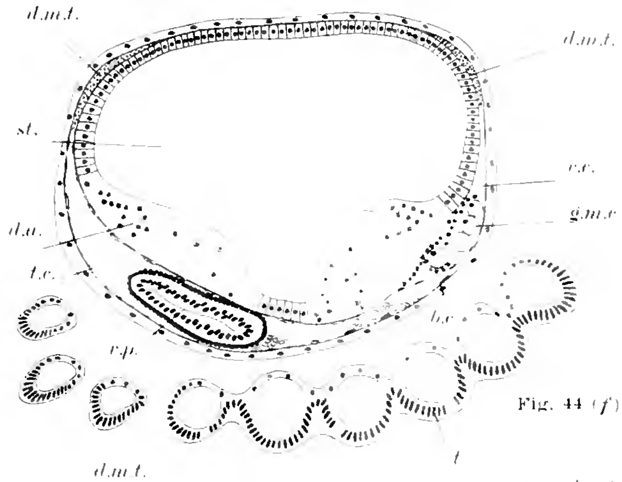


Fig. 44 (f)

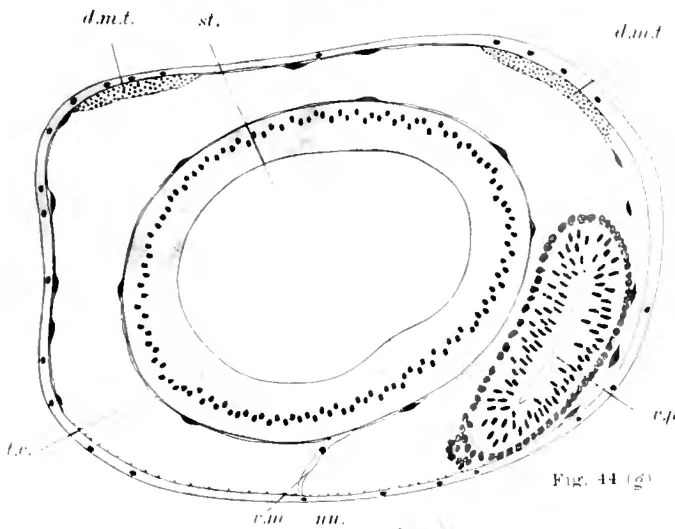


Fig. 44 (g)

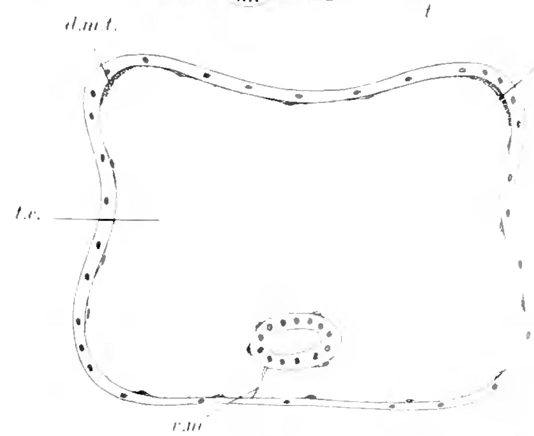


Fig. 44 (h)

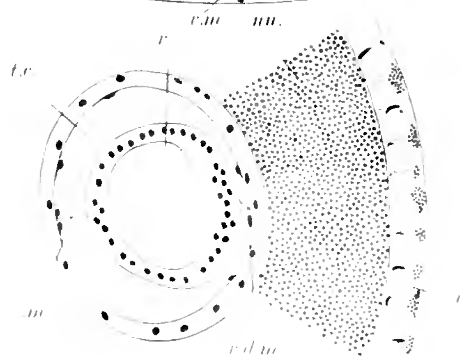


Fig. 44 (j)

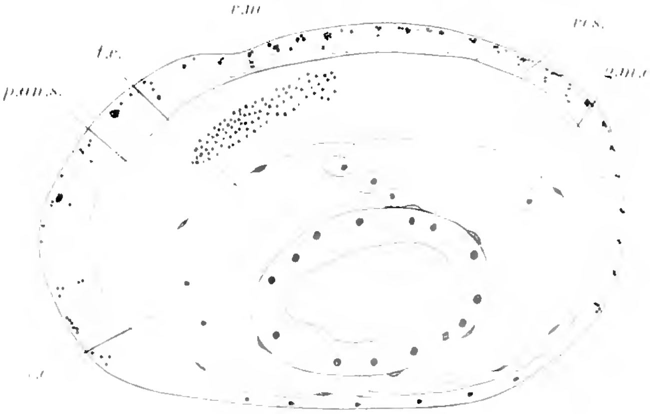


Fig. 44 (i)

PLATE IX.

PLATE IX.

FIG. 45.—Longitudinal section through the ganglion, showing lobe collar mesentery. $\frac{1}{12}$ Oil Immersion. × 4 Oc. Camera. × 293.

FIG. 45*a*.—Longitudinal section through ganglion, showing retractor and mesentery. $\frac{1}{12}$ Oil Immersion. × 4 Oc. Camera. × 293.

FIG. 45*b*.—Longitudinal section through the *Actinotrocha*, showing incomplete part of lobe collar septum. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 200.

FIG. 46.—Horizontal section through *Actinotrocha* Species B. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 200.

FIG. 47.—View showing muscles of inner surface of hood. From living specimen. $\frac{2}{3}$ Ob. × 8 Oc. Camera.

FIG. 48.—Sagittal section through *Actinotrocha* Species B. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 150.

FIG. 49.—Longitudinal section through the posterior end of *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. × 4 Oc. Camera. × 293.

FIG. 50.—Longitudinal section through *Actinotrocha* Species A., showing relations of larval collar cavity and adult collar cavity. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 200.

Fig. 45

Fig. 45 (a)

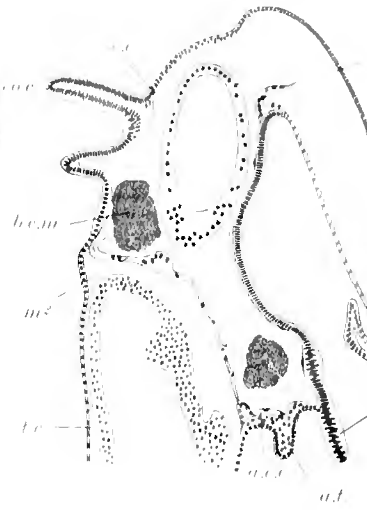


Fig. 45 (b)

Fig. 46

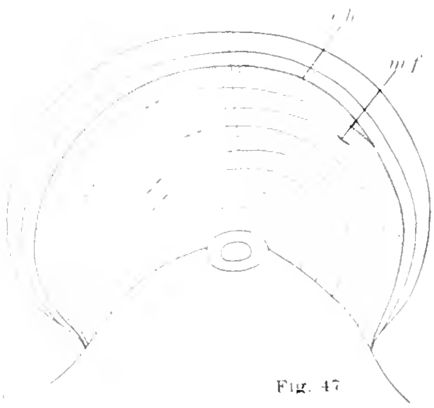


Fig. 47

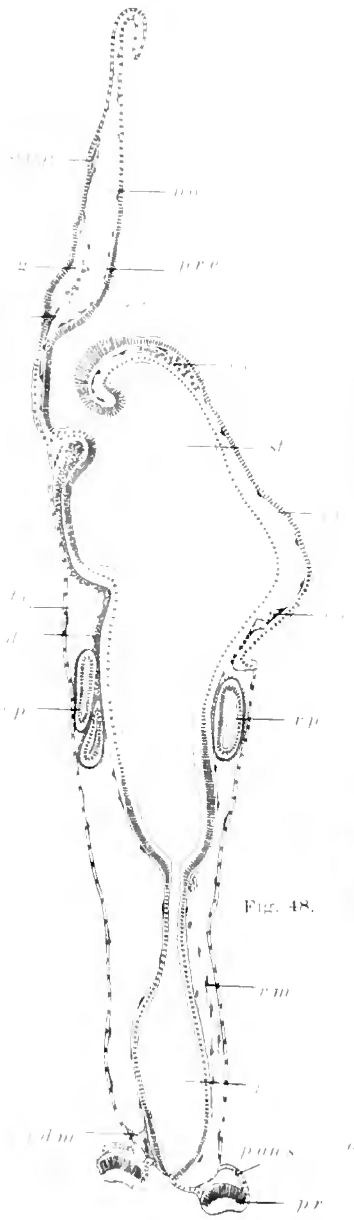


Fig. 48.

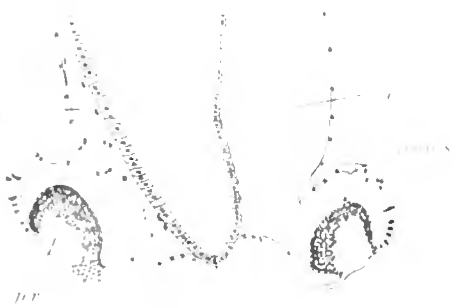


Fig. 49

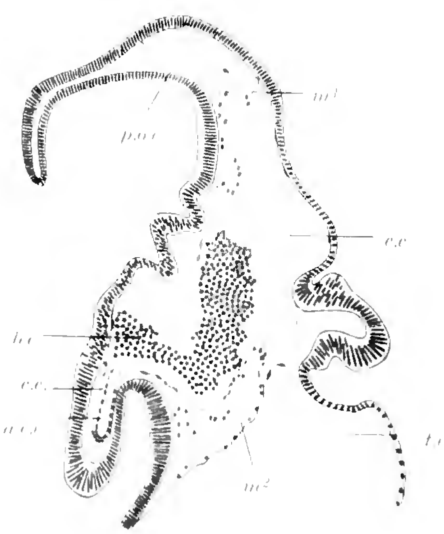


Fig. 50.

PHORONIS ARCHITECTA

PLATE X.

PLATE X.

FIG. 51.—Transverse section through *Actinotrocha* Species A. Taken through ganglion. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*a*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*b*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*c*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*d*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*e*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*f*.—Continuation of series 51. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*g*.—Continuation of series 51. Taken through the collar segment. Showing the lining drawn away from the ectodermal wall. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 51*h*.—Continuation of series 51. Taken through collar region just anterior to bases of the ventral tentacles. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 225.

FIG. 52.—Transverse section through the nephridial canal. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1400.

FIG. 52*a*.—Continuation of series 52. Taken through the lower branch of the nephridial canal. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1400.

FIG. 52*b*.—Continuation of series 52. Taken through the end of the upper branch of the nephridial canal. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.

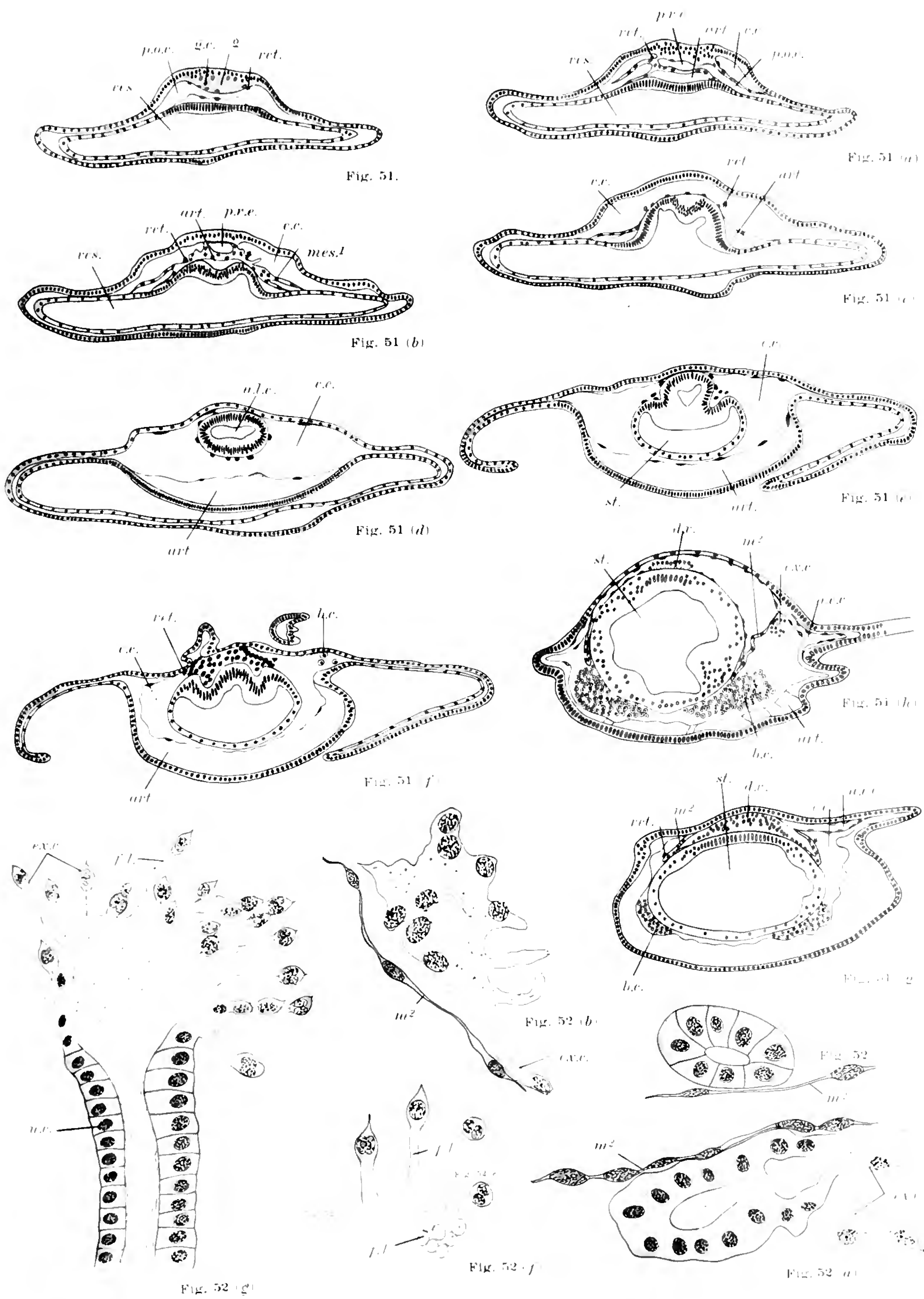
FIG. 52*c*.—Longitudinal section through one of the cellular processes at the end of the nephridium. Showing two nuclei. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.

FIG. 52*d*.—Same as fig. 52*c*. Showing one nucleus. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.

FIG. 52*e*.—Transverse section through the end of a process. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.

FIG. 52*f*.—Transverse section through the proximal half of the processes. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.

FIG. 52*g*.—Longitudinal section through anterior end of a nephridium. *Actinotrocha* Species B. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. $\times$ 1000.



PHORONIS ARCHITECTA

PLATE XI.

PLATE XI.

FIG. 53.—Transverse oblique section through *Actinotrocha* Species A. Taken through region of origin of blood corpuscles. 14 tentacles. $\frac{1}{12}$ Oil Immersion. × 4 Oc. Camera. × 293.

FIG. 54.—Transverse section through ventral collar wall. Same specimen as that of fig. 53. Showing origin of blood corpuscles. $\frac{1}{12}$ Oil Immersion. 12 Zeiss Comp. Occulare. Camera. × 935.

FIG. 55.—*Actinotrocha* Species B with ventral pouch evaginated. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 45.

FIG. 56.—*Actinotrocha* Species A. Immediately before metamorphosis. $\frac{2}{3}$ Ob. × 4 Oc. Camera. × 56.

FIG. 56*a*.—*Actinotrocha* Species A. Shortly after the beginning of metamorphosis. $\frac{2}{3}$ Ob. × 4 Oc. Camera. × 56.

FIG. 56*b*.—Metamorphosed *Actinotrocha* Species A. $\frac{2}{3}$ Ob. × 4 Oc. Camera. × 56.

FIG. 57.—Young specimen of *Phoronis architecta* (?) with 30 tentacles. $\frac{2}{3}$ Ob. × 4 Oc. Camera. × 28.

FIG. 59.—Metamorphosed *Actinotrocha* Species A. Transverse section through the region of the transverse septum. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 240.

FIG. 60.—Completely metamorphosed *Actinotrocha* Species A. Transverse section in region of branching of efferent vessel. $\frac{1}{6}$ Ob. × 8 Oc. Camera. × 240.

FIG. 61.—Adult *Phoronis architecta* removed from tube. × 8.

Fig. 53.

Fig. 54.

Fig. 55.

Fig. 56.

Fig. 56 (b)

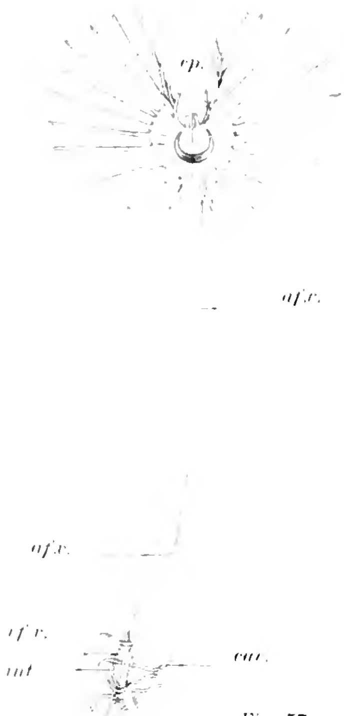


Fig. 57.

Fig. 58 (a)

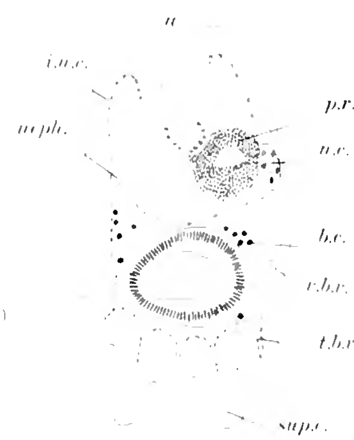


Fig. 59.

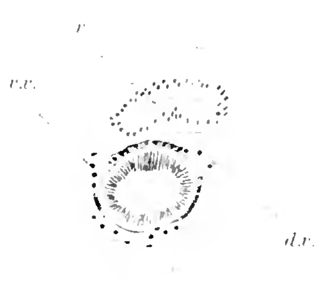


Fig. 60.

Fig. 61.

PLATE XII.

PLATE XII.

Fig. 62.—Tentacular crown of *Phoronis architecta*. Showing lophophoral organs, epistome, and mouth. Drawn from a living tentacular crown which had been constricted off from the animal. × 100.

Fig. 62

PHORONIS ARCHITECTA

PLATE XIII.

PLATE XIII.

FIG. 63.—Transverse section through *Phoronis architecta*. Taken through tentacles. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 64.—Continuation of series 63. Taken near base of tentacles. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 65.—Continuation of series 63. Taken through epistome. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 66.—Continuation of series 63. Taken through anal papilla. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 67.—Continuation of series 63. Taken through nephridial opening. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 68.—Continuation of series 63. Taken through the transverse septum and below the nephridial openings. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

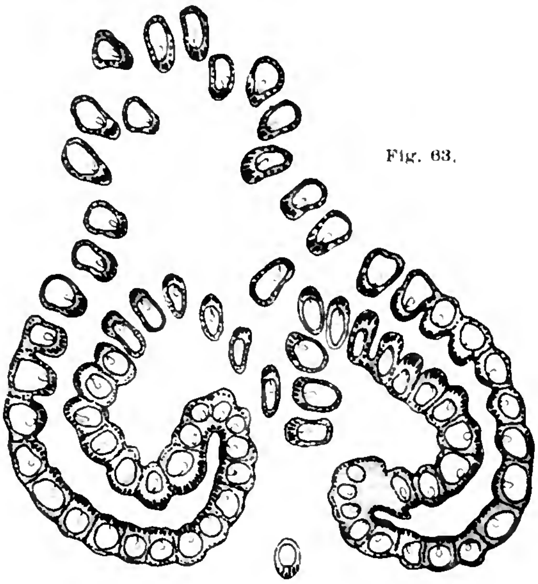


Fig. 63.

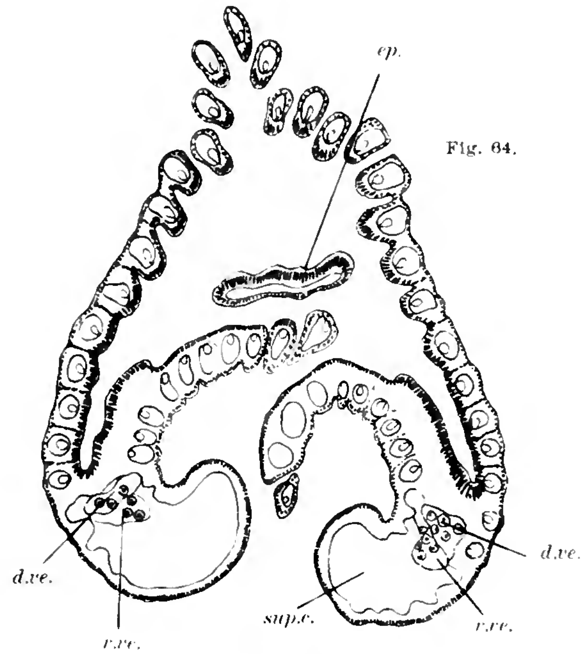


Fig. 64.

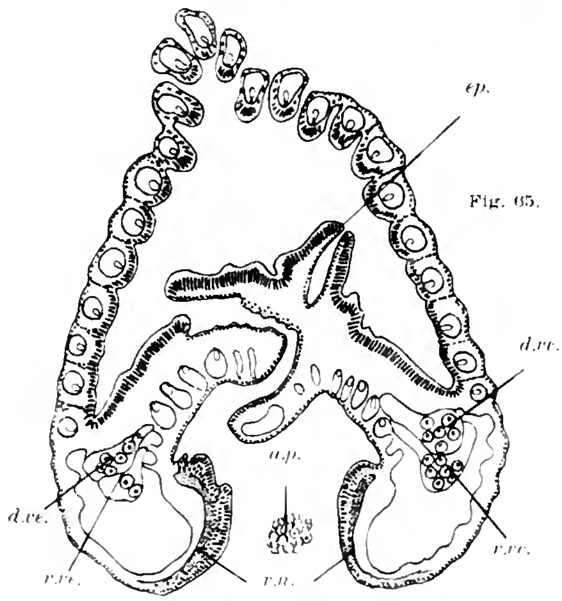


Fig. 65.

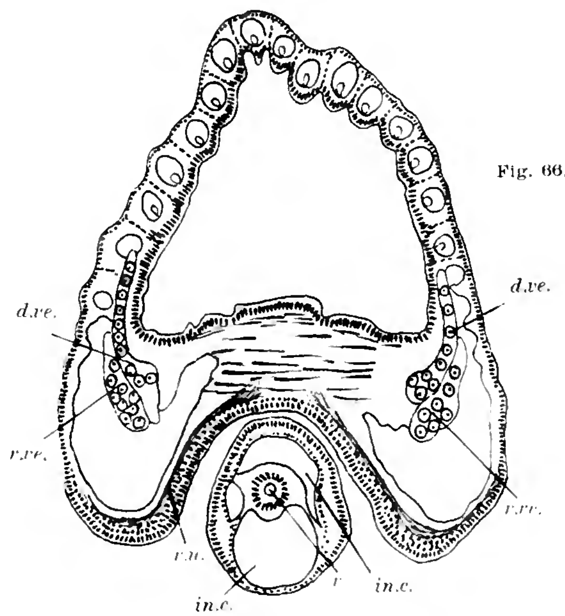


Fig. 66.

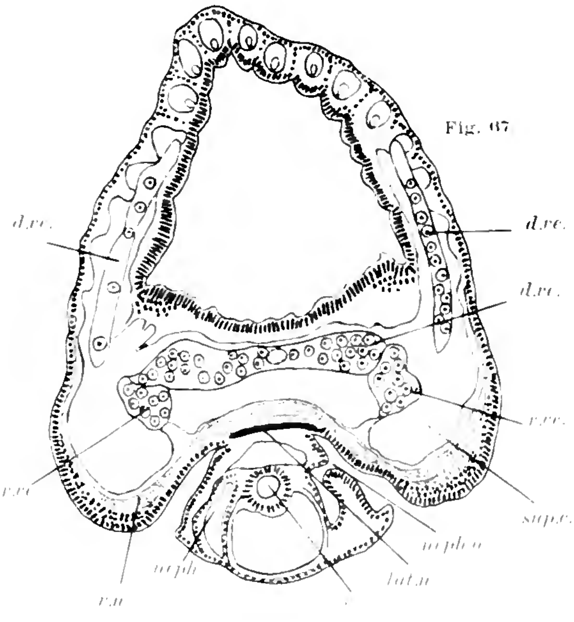


Fig. 67

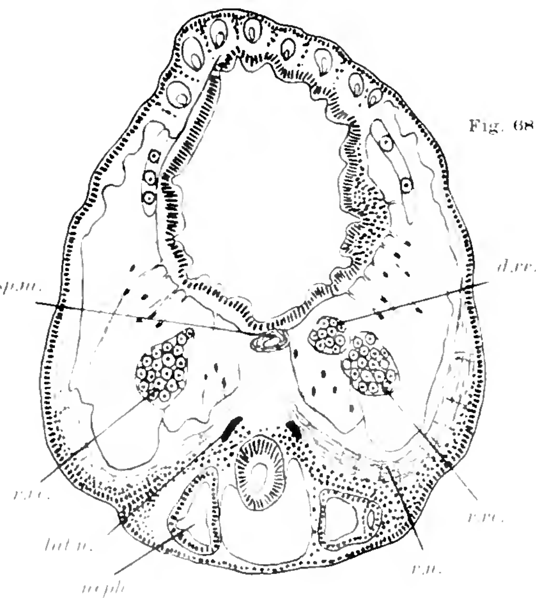


Fig. 68.

PHORONIS ARCHITECTA

PLATE XIV.

PLATE XIV.

FIG. 69.—Continuation of series 63. Taken a little posteriorly to that of fig. 68. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 70.—Continuation of series 63. Taken through the nephridial funnel that opens into the rectal cavity. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 71.—Continuation of series 63. Taken a little posteriorly to that of fig. 70. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 72.—Continuation of series 63. Taken through the funnel opening into the lateral cavity. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 73.—Continuation of series 63. Taken through the loop in the nephridium. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 74.—Continuation of series 63. Taken through the oral side of the nerve ring. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

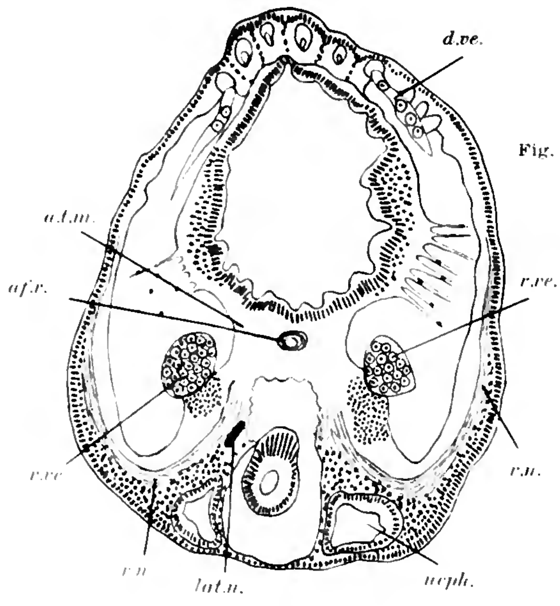


Fig. 69.

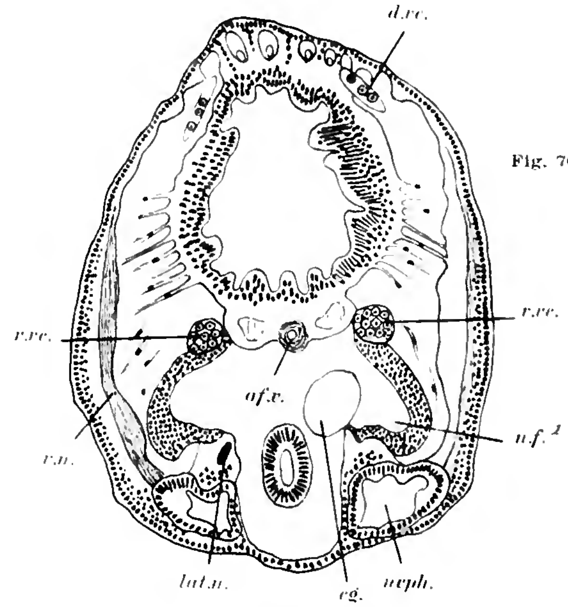


Fig. 70.

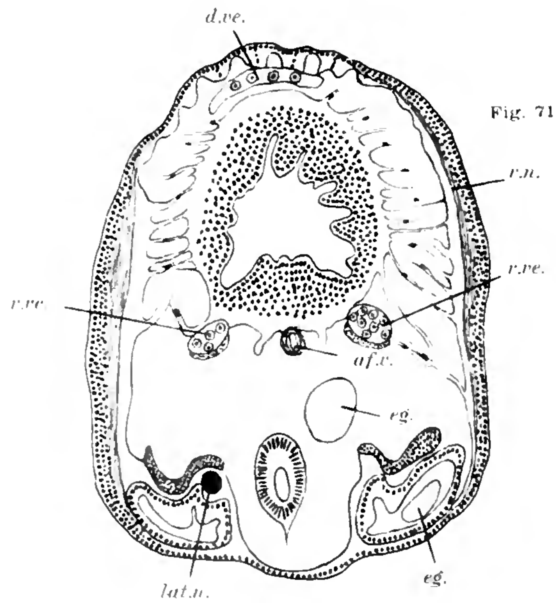


Fig. 71.

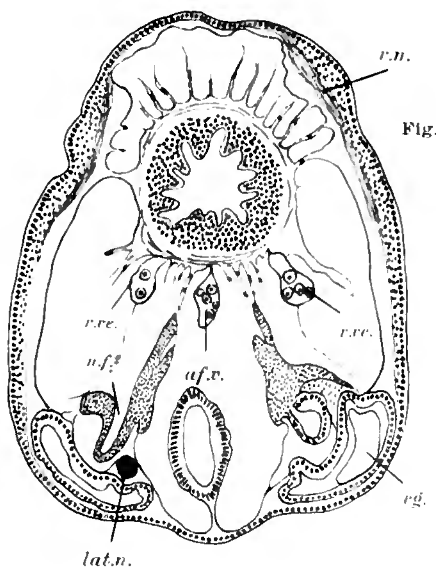


Fig. 72.

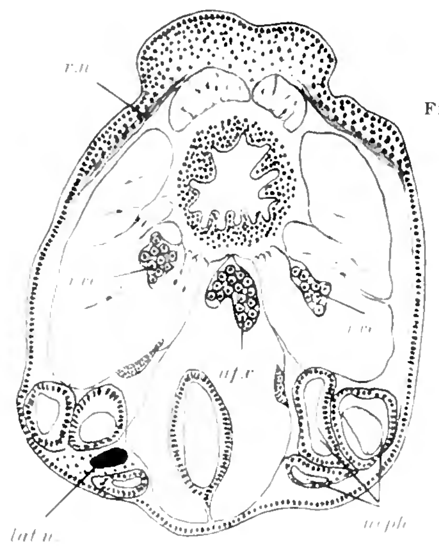


Fig. 73.

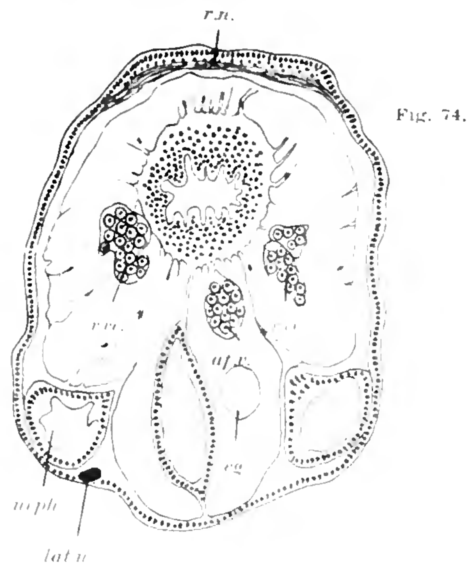


Fig. 74.

PLATE XV.

PLATE XV.

FIG. 75.—Continuation of series 63. Taken a little posteriorly to that of fig. 74. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 76.—Continuation of series 63. Taken through the region where the branches of the efferent blood vessel pass around the œsophagus. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 77.—Continuation of series 63. Taken a little posteriorly to that of fig. 76. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 78.—Continuation of series 63. Taken a little posteriorly to that of fig. 77. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 79.—Continuation of series 63. Longitudinal muscles begin to appear. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

FIG. 80.—Continuation of series 63. Taken a little posteriorly to that of fig. 79. $\frac{2}{3}$ Ob. × 8 Oc. Camera. × 130.

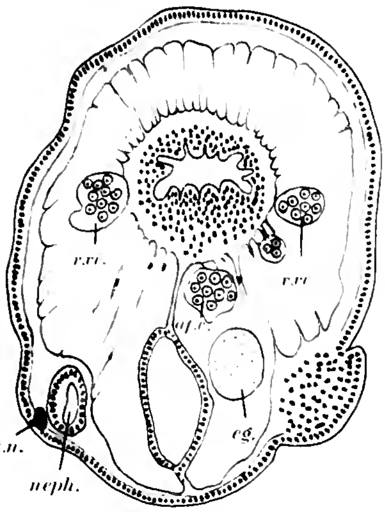


Fig. 75.

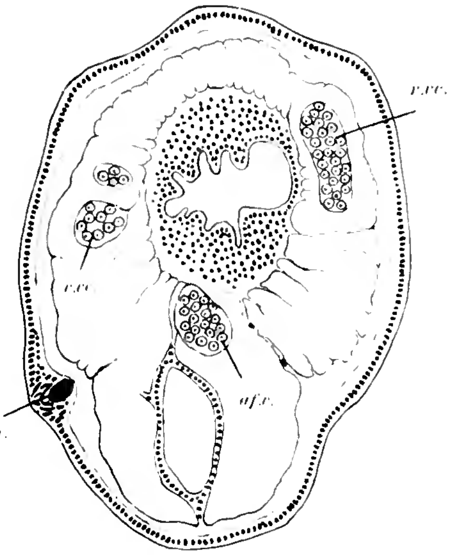


Fig. 76.

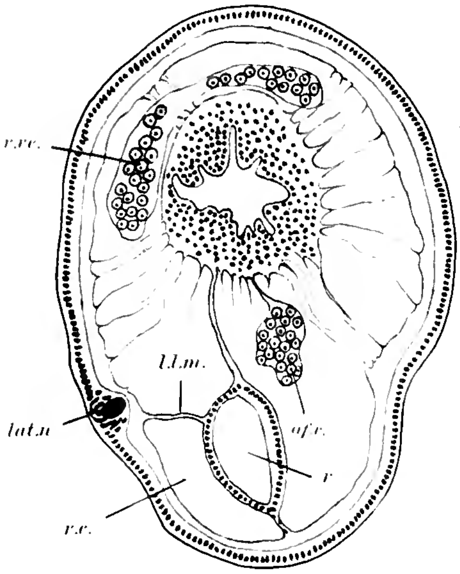


Fig. 77.

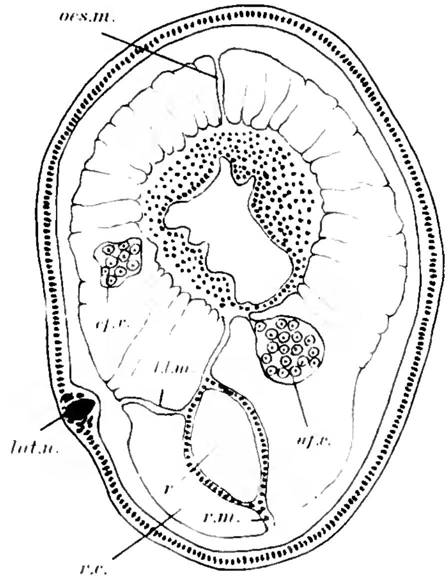


Fig. 78.

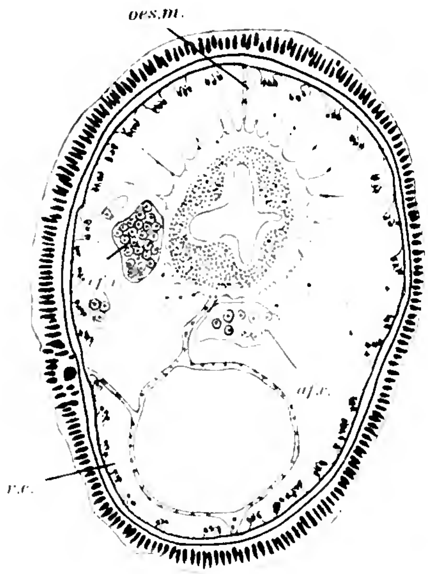


Fig. 79.

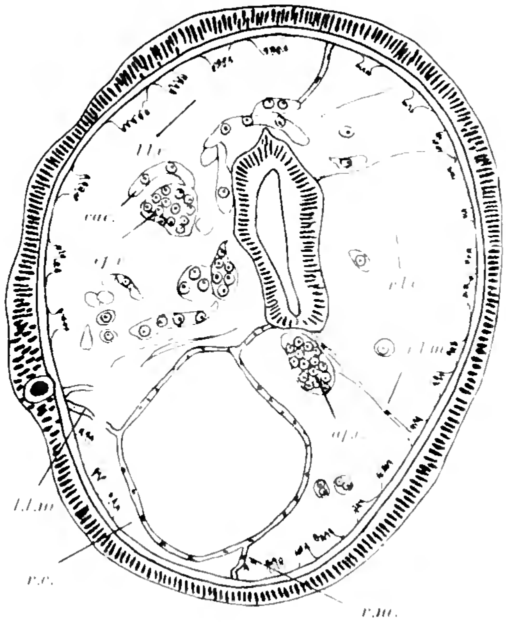


Fig. 80.

PHORONIS ARCHITECTA

PLATE XVI.

PLATE XVI.

FIG. 81.—Continuation of series 63. Taken a little posteriorly to that of fig. 80. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 82.—Continuation of series 63. Typical transverse section through the middle of the trunk. $\frac{2}{3}$ Ob. $\times$ 8 Oc. Camera. $\times$ 130.

FIG. 83.—Longitudinal section through the recipient and distributing vessels. $\frac{1}{6}$ Ob. $\times$ 4 Oc. Camera. $\times$ 450.

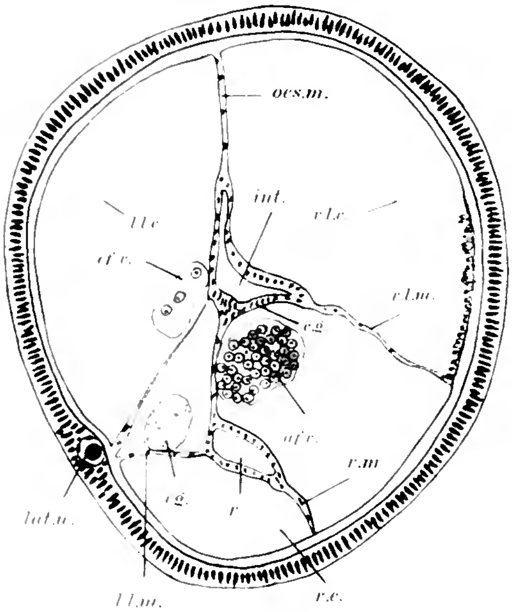


Fig. 81.

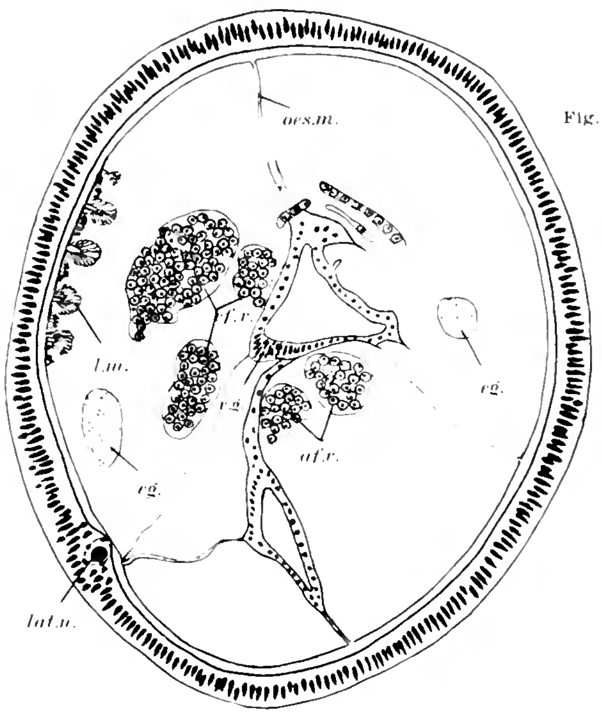


Fig. 82.

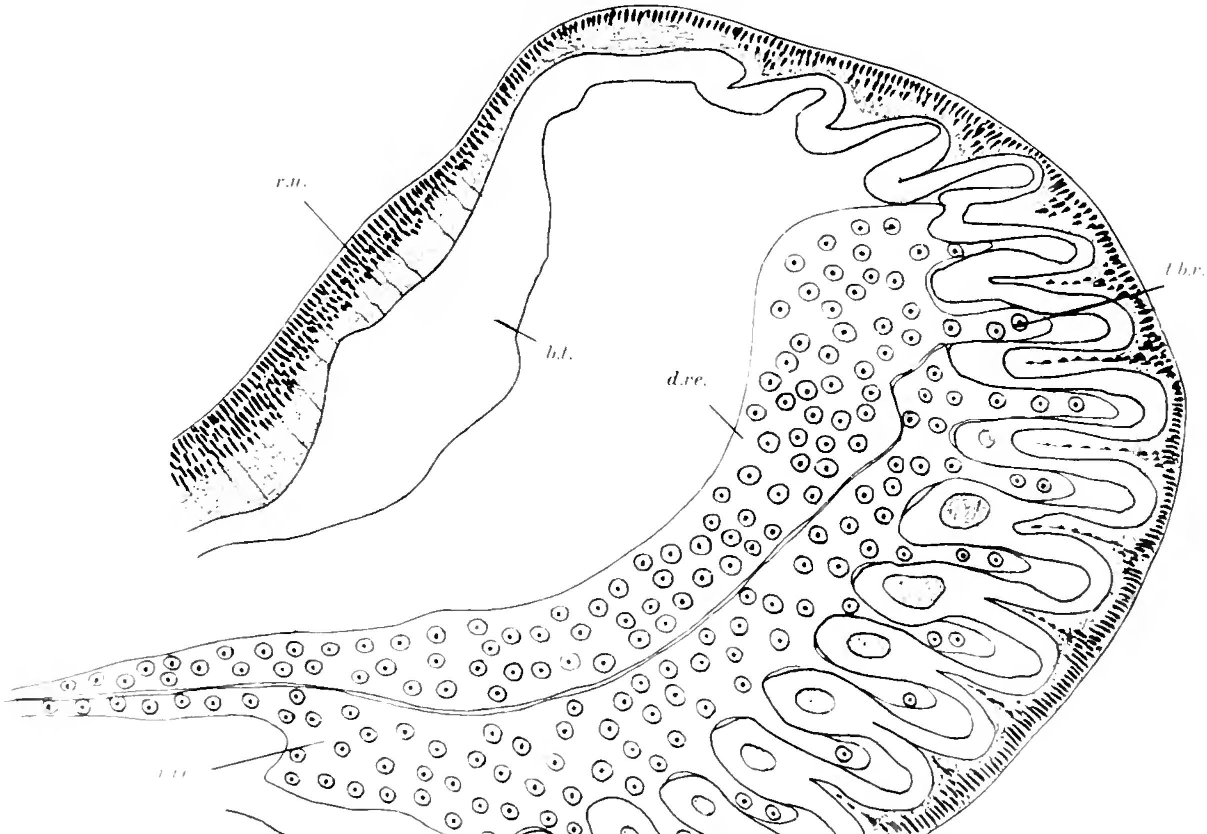


Fig. 83.

PHORONIS ARCHITECTA

PLATE XVII.

PLATE XVII.

FIG. 84.—Longitudinal section through the anal region. Showing the ganglion and its relation to the lateral nerve cord. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 450.

FIG. 85.—Transverse section through the region of the anal papilla. Showing the relation of the nerve ring to the lateral nerve. $\frac{1}{6}$ Ob. × 4 Oc. Camera. × 450.

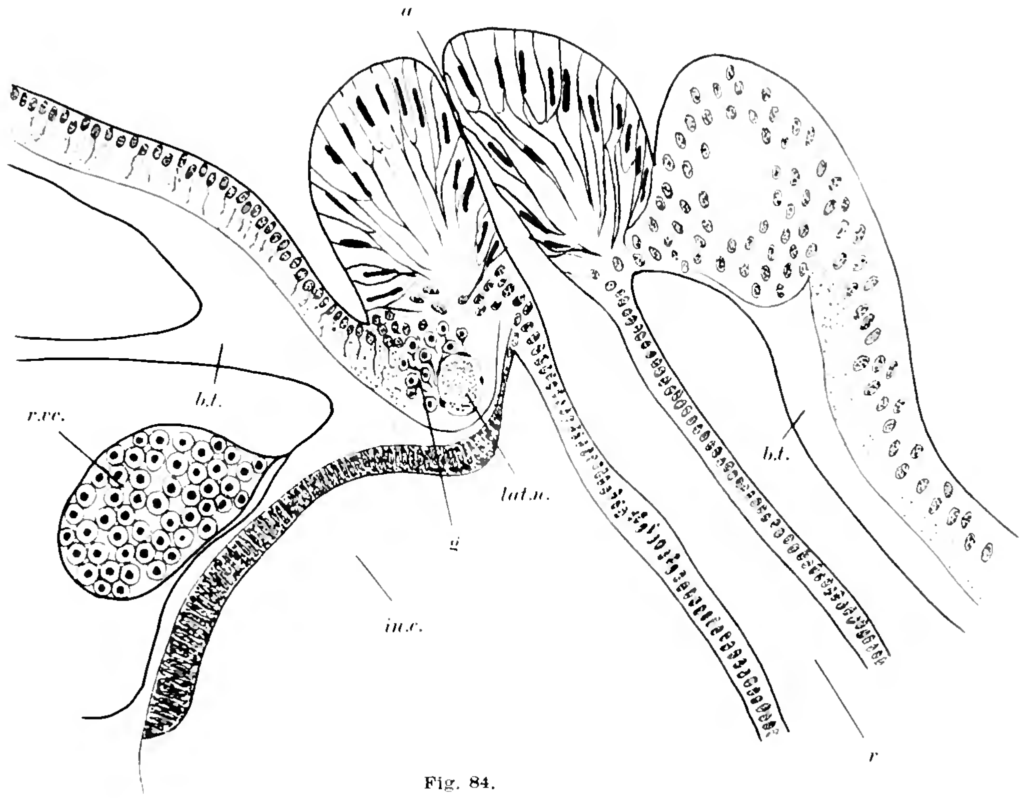


Fig. 84.

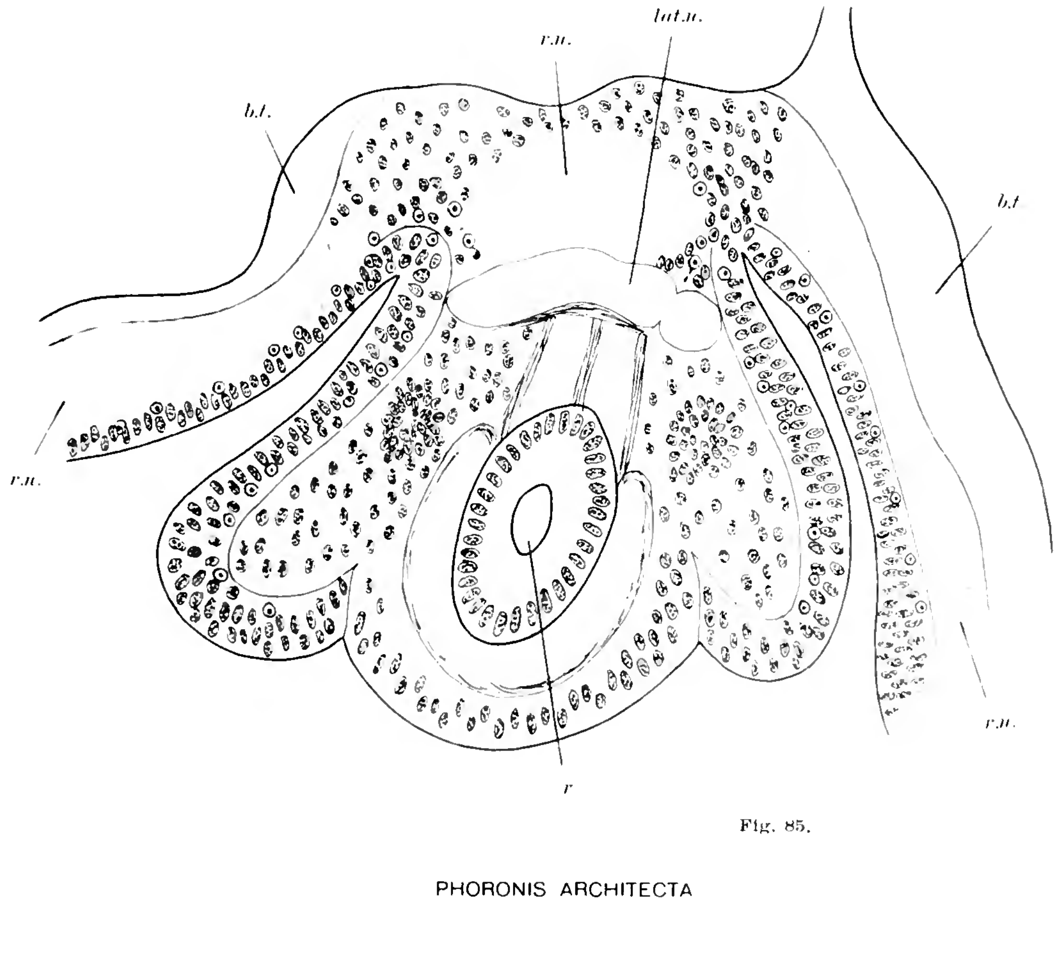


Fig. 85.

PHORONIS ARCHITECTA